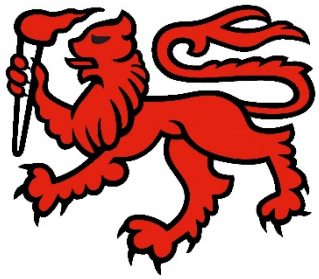

UNIVERSITY *of* TASMANIA

Reconstructing 600 years of landscape change in the grassy woodlands of the Tasmanian Midlands

Louise Romanin

BSc (Hons)

Submitted in fulfilment of the requirements for the degree of Doctor of Philosophy

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Notes on Text

This thesis consists of published papers and submitted manuscripts, therefore each chapter is set out in the style of the journal to which it has been submitted. Those chapters that have been published are inserted as copy edited PDFs. Consequently, the terminology describing the vegetation type under examination differs between chapters, there is some repetition, particularly in the descriptions of the study sites and background information regarding the study region, and there are also stylistic differences between chapters.

Chapter 3 has been accepted for publication with revision at *Australian Journal of Botany* since submission of this thesis. The revised version is included here.

Statement of Co-authorship

The following people and institutions contributed to the publication of work undertaken as part of this thesis:

Louise Romanin, University of Tasmania = Candidate

David Bowman, University of Tasmania, Supervisor = DJMB

Lynda Prior, University of Tasmania, Supervisor = LP

Grant Williamson, University of Tasmania, Supervisor = GW

Simon Haberle, Australian National University = SH

Feli Hopf, Australian National University = FH

Author details and their roles:

Paper 1, Fire regime and vegetation change in the transition from Aboriginal to European land management in a Tasmanian eucalypt savanna:
Located in chapter 2.

Candidate was the primary author and with DJMB and SH contributed to the conception and design of the research project and drafted significant parts of the paper.

Candidate contributed approximately 65% to the planning, execution and preparation of the paper SH contributed to the conception and design of the project and the analysis and interpretation of the research data. SH assisted in drafting significant parts of the paper.

DJMB contributed to the conception and design of the project and critically revised the paper FH prepared and processed pollen data for the paper.

Paper 2, Trajectory of change in land cover and carbon stocks following European settlement in Tasmania, Australia:
Located in chapter 3.

Candidate was the primary author and with DJMB, LP and GW contributed to the conception and design of the research project and drafted significant parts of the paper.

Candidate contributed 75% to the planning, execution, preparation and writing of the paper DJMB and LP made significant contributions to conception and design of the project and critically revised the paper.

GW advised on technical GIS issues for this research paper.

Paper 3, The legacy of pasture improvement causes recruitment failure in grassy eucalypt woodland conservation reserves in the Midlands of Tasmania:
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Candidate was the primary author and with DJMB and LP contributed to the planning, execution and preparation of the research project and subsequent paper submitted for publication at Australian Journal of Botany.

Candidate contributed 80% to the planning, execution and preparation of the paper.

DJMB contributed to the conception, design and interpretation of the research data, DJMB also contributed by critically revising the work.

LP significantly contributed to analysis and interpretation of the research data and with critical revisions of the paper.

We the undersigned agree with the above stated “proportion of work undertaken” for each of the above published (or submitted) peer-reviewed manuscripts contributing to this thesis:

Signed:

_____	_____
David Bowman	Greg Jordan
Supervisor	Head of Discipline of Biological Sciences
School of Natural Sciences Tasmania University of Tasmania	School of Natural Sciences University of
Date: 14 November 2018	

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Abstract

Temperate grassy woodlands are often foci for human activity. Globally these landscapes exist in a continuum from natural to synthetic. Woodlands in the Americas and Australia were occupied by humans for millennia but the transformations they effected were subtle. Woodlands in Europe have been occupied and used by humans for many thousands of years. Some landscapes have been severely degraded by human activity (e.g. the Fertile Crescent), while others exist as analogues of naturally occurring ecosystems containing a high proportion of species that are useful to humans (e.g. Dehesa of Spain). When Europeans expanded their empires they drastically altered North American and Australian woodlands to make them suitable for agriculture, creating 'Neo-European' landscapes. The Midlands of Australia is one such woodland landscape. After Europeans settled the region in the early 1800s Aboriginal land management ceased, and a suite of exotic plants and animals were introduced. In this thesis I examine landscape scale changes to the Midlands beginning in the period shortly before European arrival. Using multiple methods, I examined changes to fire regime, vegetation patterns and tree cover. I also examined the effectiveness of conservation methods in this largely privately-owned landscape, and predicted changes to tree cover under various climate change projections.

Chapter 1. Using pollen and charcoal analysis I examined how vegetation and fire regimes have changed over the last 600 years in the Midlands of Tasmania. Sediment cores from seven lagoons were sampled, with a chronology developed at one site (Diprose Lagoon) using ^{210}Pb and ^{14}C dating. Statistical contrasts of six cores, where *Pinus* served as a marker of European settlement in the early 19th Century, showed significant changes in pollen composition following settlement with (a) an influx of ruderal exotic taxa including *Plantago lanceolata* L., Brassicaceae, Asteraceae (Liguliflorae) and Rumex, (b) an increase in pollen of the aquatics *Myriophyllum* spp. and Cyperaceae, (c) a decline in native herbaceous pollen taxa, including Chenopodiaceae and Asteraceae (Tubuliflorae) and (d) a decline in *Allocasuarina* and an initial decline and then increase of Poaceae. The presence of Asteraceae (Liguliflorae) in the pre-European period suggests that an important root vegetable *Microseris lanceolata* (Walp.) Sch.Bip. may have been abundant. Charcoal deposition was low in the pre-European period and significantly increased immediately after European arrival. Collectively, these changes suggest substantial ecological impacts following European settlement including cessation of Aboriginal traditions of fire management, a shift in hydrological conditions from open water lagoons to more ephemeral herb covered lagoons, and increased diversity of alien herbaceous species following pasture establishment

Chapter 2. The Midlands of Tasmania is a valuable model system for studying changes to tree cover and above ground biomass in neo-European landscapes. Aerial imagery, historical reconstructions, field surveys and future climate projections provided tools to chart changes in tree canopy cover and carbon stores in the Northern Midlands for the period 1788–2070. In the 160 years between 1788 and 1940s, large areas of

open woodland were cleared but carbon loss was modest (-14 %). In the 60 years between 1940s and 2010, carbon loss accelerated (a further -21%) as clearing shifted from woodlands to forests. An estimated 28% of the study area would need to be replanted with eucalypts to capture the carbon lost between 1788 and 2010. Three general circulation models (GCMs) representing climate predictions for 2070 suggest that carbon storage in the landscape would change by +13% to -13.2% of 2010 levels, without any restoration intervention.

Chapter 3. The Tasmanian Midlands is now primarily privately owned, with very little area devoted to conservation of biodiversity. In this landscape, conservation covenants have been enacted on many private properties with the intention of encouraging tree recruitment and conservation of threatened plant communities and rare species. I compared the demographic structures of overstorey *Eucalyptus* species and midstorey tree genera on public and private properties with contrasting land use histories. Reserves on private lands had little tree recruitment, probably because exotic pasture species were common, whereas tree recruitment was abundant in public reserves, where pasture improvement has not occurred. Active measures are needed to restore ecological structure and function in grassy woodland conservation reserves on private land by encouraging regeneration of *Eucalyptus* and *Acacia* as well as returning the understorey to a functionally native state. This will entail reinstating fire disturbance, reducing exotic pasture species cover and managing domesticated (sheep), feral (deer) and native (macropod) herbivores.

Synthesis. The landscape of the Midlands has been subject to phases of alteration according to the needs and values of its human inhabitants throughout time. The ways that humans have manipulated the landscape have interacted with available technologies and climatic conditions. Early Aboriginal inhabitants arrived in Tasmania during a time of glaciation and used fire to manipulate the landscape. Modern Tasmanians now live in a rapidly warming climate and possess a broad suite of technologies to cultivate, fertilise and irrigate the landscape. The drive to increase productivity conflicts with a desire for healthy landscapes. However, inhabitants of the Midlands see value in biodiversity and ecosystem function, and landowners and conservation agencies are working together to create a healthy landscape that will function under future climate conditions

General introduction

Temperate grassy woodlands as a distinct global community

Temperate grassy woodlands are a vital component of the earth's ecosystem. They provide highly favourable climatic and environmental conditions for humans and as such have been heavily impacted by human habitation and are often degraded or under threat. Despite their importance there is a lack of a clear definition of the character and extent of temperate grassy woodlands. In this chapter, I will use vegetation physiognomy and climate to establish a definition of temperate grassy woodlands. I will then examine recent changes in and possible futures of this biome utilising the Midlands of Tasmania as a microcosm of temperate grassy woodlands worldwide.

Grass/tree coexistence

To understand the dynamics of grassy woodlands it is important to understand the co-dominance of grasses and trees. Interactions between grass and trees are not completely understood but they are generally believed to have a competitive relationship (Scholes and Archer 1997). Grass can inhibit the establishment of trees *via* competitive effects and by promoting regular fire. Trees can inhibit the growth of grass by being strong competitors for water and nutrients and creating shade which can prevent grass growth (Scholes and Archer 1997). Several models attempting to explain the co-occurrence of trees and grass have been developed (see House *et al.* 2003). However, none provide a satisfactory explanation of grass-tree dynamics in all regions. It is likely that combination of competition and facilitation between the dominant life forms as well as climate, edaphic factors and disturbance all combine to create a mix of grass and trees that is stable, at least in the short term (House *et al.* 2003).

Areas where grasses and trees coexist occupy large areas of the globe described by Whittaker (1975) as 'ecosystem uncertain' given that climate and edaphic factors could support forest or grassland. Temperate grassy woodlands exist within these 'ecosystem uncertain' areas in an apparently stable state, with this apparent stability explained in part by disturbance in the form of herbivory or fire, which Bond (2005) has described as 'consumer controlled'. Vegetation consumers can be either biotic (herbivores) or abiotic (fire) (Bond 2005). Mammalian herbivores can consume tremendous amounts of vegetation and in their absence, it is suggested that fire can replace their herbivory effects. However, unlike herbivores, fire is non-selective in its consumption of plant biomass. This means that the patterning of vegetation structure is

different according to whether abiotic or biotic consumers create the largest impacts (Bond and Keeley 2005; Bond *et al.* 2005).

Fire is an important factor in the coexistence of grasses and trees. Burning may promote a flammable landscape where the climate could support fire resistant forest (Bond *et al.* 2005). The tropics and southern hemisphere support ecosystems which burn more frequently than those in temperate and boreal areas of the northern hemisphere. Without burning, vegetation complexes with C_4 grasses would transform to closed angiosperm forest (Bond *et al.* 2005). The same study found that ecosystems with C_3 grasses are less dependent on fire and with less area converted to forest in the absence of fire.

Fire exclusion studies can elucidate the effect fire has on a landscape. Bond et al. (2005) describe three patterns of response to fire suppression 1) if no vegetation change occurs, the vegetation is climate limited, 2) if woody plants increase in density or size but no changes in species composition are found, the vegetation is climate limited and modified by fire, 3) if density and size of woody plants increases and there is a successional tendency to forest with invasion of fire sensitive trees and shrubs, the vegetation is fire limited.

In addition to disturbance by fire and mammalian herbivores, insect herbivores, drought, cyclones and flooding can play important roles in maintaining an open woodland structure. Tree growth can also be limited by soil structure and fertility (Lehmann *et al*. 2011). Low temperatures and frost can inhibit tree growth and cause inverted treelines (Patton 1988). Insect outbreak within forests (Kurz and Apps 1999; Metsaranta *et al.* 2010) or seasonally inundated and poorly drained soils can also limit the growth of trees (Veldman *et al.* 2015).

Grass/tree vegetation types

The difference between temperate grassy woodlands, tropical savanna and forest-steppe can be attributed in the most part to differences in climate. The differences in climate alter species composition, growing season, productivity, and disturbance regimes. Despite very similar physiognomy, climatic difference is great enough to clearly separate temperate grassy woodlands from the other two vegetation units as outlined below.

Tropical savanna

Unlike in temperate grassy woodlands, temperatures in tropical savannas are high throughout the year. Much like Mediterranean climates, rainfall is highly seasonal in tropical savanna, but the period of prolonged drought occurs in winter instead of summer (Peel *et al.* 2007). The savannas of xeric regions support understoreys comprised of shrubs so are not comparable to temperate grassy woodlands. In mesic savanna areas, summer-growing C_4 grasses proliferate, so highly flammable biomass rapidly accumulates (Lehmann *et al.* 2011). This rapid annual accumulation of herbaceous biomass often supports high herbivore loads (Bond *et al.* 2005). Additionally, the amount of rainfall heavily influences the density of woody vegetation with savanna transitioning to forest in mesic climates and from savanna to shrubland or spinifex grassland in semi-arid areas (Scholes and Archer 1997; Lehmann *et al.* 2011). The same pattern of rainfall-influenced tree density is observed in some temperate grassy woodlands (Joffre *et al.* 1999). A prolonged dry period means that trees experience annual water stress, thus limiting tree density.

There are similarities between temperate grassy woodlands and tropical savannas in the disturbance dynamics governing the coexistence of grasses and trees (Scholes and Archer 1997; Higgins *et al.* 2000; Jeltsch *et al.* 2000). The most important driver of tropical savanna structure is the regular and extensive fires that occur, most often in autumn-winter. Savanna fires occur at between 2 – 5 year return interval (Hutley *et al.* 2013; Murphy *et al.* 2013). In fact, fire is more important than climate in determining the presence of grass in mesic savannas (Bond *et al.* 2005). There is ample evidence that fire is also important in temperate landscapes, but ecosystems with C_3 grasses are less dependent on fire to remove biomass than tropical ecosystems (Bond *et al.* 2005). The speed at which dry biomass accumulates in temperate grassy woodlands is much slower than in mesic tropical landscapes, therefore the fire return interval is much longer (Murphy *et al.* 2013).

Due to high year-round temperatures, invertebrate fauna, particularly termites, ants and grasshoppers, can play important roles as grazers and seed predators in tropical savannas. Invertebrates may selectively decrease either grassy or woody biomass (Andersen and Lonsdale 1990). Cyclones and storms in Australia's

tropical savannas can result in severe and widespread structural damage mostly affecting woody species (Hutley *et al.* 2013).

Forest-steppe

Forest-steppe forms an ecotone between true steppe and forests. It comprises forest patches in a mosaic of grassland in cool-temperate regions of Eurasia, South America and northern North America with a strongly continental climate. Winters are very long and cold causing soils to freeze. Soil geoturbation caused by frost heaving is influenced by many factors including soil moisture, soil texture, vegetation cover and depth of snow cover, and can negatively affect the survival of both grasses and tree seedlings (Biswell *et al*. 1953; Goulet 1995). The difference between summer and winter temperatures is great resulting in a short growing season. Annual precipitation is low (210 – 860 mm) and, in some regions, a large proportion of rainfall occurs in summer (Erdős *et al.* 2018). Productive soils and favourable summer conditions mean that net primary production, biomass accumulation and carbon sequestration is very high compared to other non-tropical systems (Erdős *et al.* 2018). Like many tropical savannas, forest-steppe supports a high herbivore load. Unlike temperate grassy woodlands, forest-steppe regions can have some of the highest soil fertility in the world (Faber-Langendoen *et al.* 2012).

Physiognomy of forest-steppe is maintained by grazing, the short growing season and water deficits. Soils play a particularly important role in determining physiognomy with the steppe component usually found on different soils to the forest component. Soils with low water retention capacity limit tree growth (Dulamsuren *et al.* 2005; Erdős *et al.* 2018). High soil temperatures in summer may also limit germination of tree seeds and therefore the spatial extent of trees in the landscape (Dulamsuren *et al.* 2005).

Erdős *et al*. (2018) proposed that forest-steppe of Eurasia includes eastern European forest-grassland macromosaics and open woodlands of the Middle East which have a Mediterranean-influenced climate. In Europe and North America, steppe forms the northern continuation of continental grassland and temperate grassy woodland type vegetation. In Europe there is evidence that the grasslands/woodlands of some regions of central Europe have persisted continuously since the Pleistocene when steppe

environments would have extended further south than they do in modern times (Jørgensen and Quelch 2014; Pokorný *et al.* 2015).

Temperate grassy woodland

Temperate grassy woodlands lie within the climatic conditions classified in the Köppen-Geiger C zone, but are confined to areas where the annual rainfall is 250 – 1250 mm (Whittaker 1975), annual temperature is 5 – 18 °C and mean temperature of the coldest month is 0 – 18 °C (Peel *et al.* 2007). Less is known about temperate grassy woodlands than tropical savannas and a fuller discussion of temperate grassy woodlands follows.

Defining temperate grassy woodlands

There is no global definition of what constitutes a temperate grassy woodland. Differences in terminology hinder a global synthesis of research into one vegetation type. Without an agreed definition and structural framework, it is impossible to determine the dynamics that influence the biome in any universal sense or provide prescriptions to effectively manage their persistence into the future.

Part of the difficulty in defining the global distribution of temperate grassy woodlands is that terminology varies widely throughout the literature. Temperate grassy woodlands are known by various terms around the world; 'grassy woodlands' in southeast and southwest Australia (Yates and Hobbs 1997a), 'wood-pastures' in continental Europe (Bergmeier *et al.* 2010), 'dehesa' in the Iberian Peninsula of Spain (Olea and San Miguel-Ayanz 2006), 'montado' of Portugal (Joffre and Rambal 2006), and 'oak savanna' or 'open woodlands' (Taft 1997) and 'pine savannas' in North America . They are also variously known as 'tree savanna', 'open woodland' and 'rangeland'. The temperate grassy woodlands of southeast Australia are sometimes referred to as 'savanna woodlands' or 'temperate savannas,' although some suggest that the term savanna only be used in reference to tropical systems (Beard 1967) with summer growing C_4 grasses (Ratnam *et al.* 2011). To solve this confusion of terminology, I will define temperate grassy woodlands by reference to a specified type of vegetation physiognomy which occurs in climactically temperate zones.

Physiognomy of temperate grassy woodlands

Despite differences in nomenclature, the basic structure of temperate grassy woodlands is characterised by widely spaced trees over a continuous herbaceous/graminoid layer. Exactly how much cover 'widely spaced trees' provide differs substantially between vegetation classification schemes (Figure 1). In Australia the terminology specifies that the crown of trees does not touch (Yates and Hobbs 1997a). This spectrum of temperate grassy woodland definitions means there is no global consensus on the limits of tree height and canopy cover. Terminology is similar in western United States and British colonies, but in eastern United States and the British Isles 'woodland' is a synonym for forest (Eiten 1992). The lower limit for open-woodland or woodland tends to be 10% canopy cover, but the upper limit is much more variable, ranging from 30% (Specht and Specht 2013) to 90% at the extreme (Nelson 2004). The lack of consistency in defining an upper limit of canopy cover is because temperate grassy woodlands occur in a physiognomic continuum between forest and grassland. This chapter uses the commonly agreed lower limit of 10% canopy cover and adopts an upper limit of 60% as being intermediate between upper canopy cover limits as described in the literature. This percentage is consistent with 'widely spaced' overstorey.

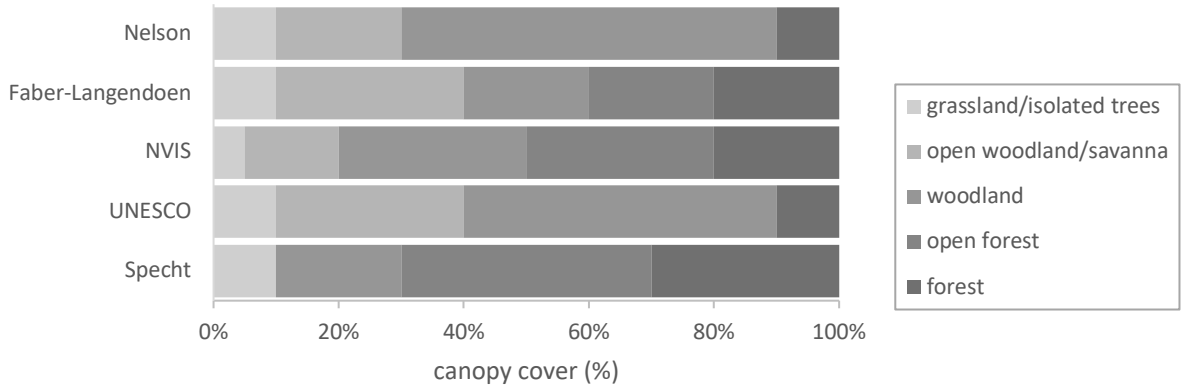

Figure 1. Comparison of differences in tree canopy cover in a selection of classification systems in the continuum between grassland and closed forest. Nelson (Nelson 2004)*, Faber-Langendoen* (Faber-Langendoen *et al.* 2014)*, NVIS* (NVIS Technical Working Group 2017)*, UNESCO* (UNESCO 1973)*, Specht* (Specht and Specht 2013)*. Adapted from Taft* (1997)*.*

Unlike overstorey definitions, ground layer definitions are consistent. A continuous ground layer of grasses and herbs with few shrubs is agreed upon in most instances. I use the term 'grass' to refer to graminoids and include herbaceous forbs in the matrix. Temperate grassy woodlands may have C_3 and/or C_4 grasses in the ground layer. In denser temperate grassy woodlands, C_3 grasses will dominate and shrubs may become more common (Taft 1997). In colder and wetter climates graminoids may be less common and sedges

dominate (Fletcher and Thomas 2010). The ground layer of temperate grassy woodland is often influenced by adjoining vegetation types. This will be discussed later in the section on transition zones.

Woodlands with a significant ground layer of shrubs or sedges have been excluded from this definition because a shrubby or sedgy ground layer responds to environmental influences such as grazing or fire in a different manner to a grassy ground layer. In addition, shrubs tend to be found in drier areas and on nutrient poor soils (Specht 1969) or in vegetation with more canopy cover than temperate grassy woodland (Taft 1997). Shrubby woodlands were therefore much less favoured for agricultural development.

Climate

The term 'temperate' can be defined based on temperature or latitude, we choose here to use the Köppen-Geiger climate-based definition. The Köppen-Geiger C zone includes parts of warm and cool temperate regions, including Mediterranean landscapes (30° – 40° north and south). It excludes zones that have a severe winter with long periods of snow as these conditions alter vegetation dynamics sufficiently to inhibit the establishment of temperate grassy woodlands (Kirkpatrick and Bridle 2013). Mediterranean landscapes are found on the west coasts of continents and experience hot, dry summers and cool, wet winters (Köppen-Geiger climate zones Csa and Csb). Mediterranean landscapes include those in the Mediterranean basin, California, southwest Western Australia, southern South Australia, and Chile (Faber-Langendoen *et al.* 2012). Temperate grassy woodlands are also found in some warm to cool temperate regions such as is found in eastern Europe, the Midwest of the United States and southeast Australia. These areas have moderately low annual rainfall and a strong contrast between summer and winter temperatures but do not have a severe winter (Köppen-Geiger climate zones Cfa and Cfb) (Peel *et al.* 2007). In temperate regions rainfall may be evenly distributed throughout the year (Prober and Thiele 2005; Specht and Specht 2013) or may be seasonal (Joffre *et al.* 1999).

Transition zone

One of the major difficulties in defining temperate grassy woodlands is their position in a transitionary zone between forests and grasslands. Boundaries between forests and temperate grassy woodlands or grasslands and temperate grassy woodlands are complicated, gradual and hard to define (Davies 1964).

Within a transition zone, the balance between trees and grass can change rapidly over space and time depending on disturbance (Platt *et al.* 2006). Some mapping of grassland and forest boundaries may appear clearly defined, but this is for reasons of convenience because it is difficult to map complicated and variable transition zone vegetation (Taft 1997). Some examples of transition zones include the pinyon woodland/savannas of Texas which form an intermediate between grasslands and deciduous forests (Caldwell *et al.* 2008).

Within North America, the oak woodlands of the Midwestern states occupy a transitional position between Great Plains prairies of central USA and oak forests of the east, exhibiting strong compositional affinities with prairie or grassland (Nelson 2004; Wessman *et al.* 2004). Within the Southern Hemisphere, the temperate grassy woodlands of Australia form a transition between wetter forests in coastal regions and the grasslands and shrublands of the arid interior (Department of the Environment and Water Resources 2007). In southwest Australia however, TWINSPAN analysis was unable to distinguish between temperate grassy woodland and open-forests possibly because these woodlands exist as extensions of forest into less favourable sites (Specht et *al*. 1995; Yates and Hobbs 1997a; Specht and Specht 2013).

Even at the cold climate extremes of woodlands, forest-steppe landscapes occupy the position between treeless steppe and closed forests (Erdős *et al.* 2018). Cultural wood-pastures in Europe form an ecotone between forest and grassland (Bergmeier *et al.* 2010). By contrast, the cultural temperate grassy woodlands of Spain do not appear to be a transitional vegetation type, perhaps explained by their long history of human modification and maintenance and a harsh Mediterranean climate.

Disturbance in temperate grassy woodlands

Disturbances caused by fire and herbivory are common in temperate grassy woodlands and have been identified as important for maintaining the balance between grass and trees in many regions. In European wood-pastures, grazing of domestic herbivores and traditional coppicing of trees maintains structural composition (Erdős *et al.* 2017). Fire can be carefully used in pasture management of wood-pastures in eastern Europe, but uncontrolled fire damages trees and causes a transition from woodland to grassland (Hartel *et al.* 2013). In the temperate grassy woodlands of Australia and North America, fire and grazing

prevent thickening of trees, encroachment of shrubs or over dominance of grasses (Taft 1997; Watson and Morris 2006). Both regions have a long history of indigenous land management involving fire to maintain vegetation structure (Bowman 1998; Keeley 2002) suggesting that the vegetation is well adapted to persist under this regime of low intensity burning.

However, the pattern within Australia and western USA is complex because grazing and inappropriate fire regimes can also promote woody plant encroachment (Belsky and Blumenthal 1997; Eldridge and Soliveres 2014). Large, high intensity bushfires can promote mass germination of some shrub species which replace the grassy ground layer (Harrington *et al.* 1979). Direct paleological evidence from the highland grasslands of Tasmania shows an invasion by shrubs concurrent with an increase in grazing by stock (Thomas and Hope 1994). Overgrazing reduces competition from grasses which can allow shrub and tree seedings to establish at higher densities than usual (Belsky and Blumenthal 1997). Many of the shrubs that establish are not palatable to stock so go on to establish widely (Harrington *et al.* 1979). Trampling, soil compaction and erosion can also play a role in altering the physiognomy of temperate grassy woodlands (Harrington *et al.* 1979).

Cultural landscapes

A long history of human occupation, and subsequent manipulation of the land, means that temperate grassy woodlands are cultural landscapes. Temperate grassy woodlands have a long history of human land use with varied outcomes. From the woodlands of the Fertile Crescent in the Middle East where agriculture evolved (Lev-Yadun *et al.* 2000) to the woodlands of southeast Australia where Aborigines hunted kangaroos for millennia (Tindale 1959; Cosgrove and Allen 2001; Pascoe 2014), humans have been drawn to these regions and used them to support productive lifestyles.

The focal areas for historical agricultural development tended to occur in regions of grassland or grassy woodland where temperature and precipitation were just right for agriculture, not too wet, too dry or too cold (Ewel 1999). The Fertile Crescent in the Middle East was once covered with Mediterranean woodland containing the progenitors of many important modern crops. Approximately 10,000 years ago it became the site of early domestication of grasses, legumes, and figs (Lev-Yadun *et al.* 2000) and thus a focus of

human activity. The region is now so altered that many wetlands have disappeared and the region is prone to regular and harsh drought; over exploitation of the environment has created degradation and propensity to desertification (Diamond 1994; Nielsen and Adriansen 2005).

Likewise, Anasazi cities in New Mexico (900-1300 AD) were once pinyon/juniper woodlands and were also exploited for woodland resources (Diamond 1994). Irrigated agriculture, firewood harvesting, and timber extraction combined with long-term drought wrought drastic ecological change leading to societal and environmental collapse (Maliva and Missimer 2012). A harsh, dry climate means that trees, even to present time have not regrown (Swetnam *et al.* 1999). In more recent times, during the 18th and 19th centuries Europeans colonised already occupied landscapes. The temperate grassy woodlands of North America and Australia became targets for new settlements and were transformed to suit European style pastoralism and agriculture commencing fragmentation and degradation of the landscape which continues to today (Prober and Thiele 1995; Rhemtulla *et al.* 2007). In contrast, silvopastoral landscapes, which mimic natural woodlands, have existed as productive and stable systems around the Mediterranean Sea for many hundreds of years (Joffre *et al.* 1999).

While human use of woodland landscapes has sometimes resulted in catastrophic collapse, this is not always the case. Some temperate grassy woodland landscapes have been used to satisfy human needs for so long that they have been transformed to a stable alternative state (Westoby *et al.* 1989). Indeed, it can be argued that that the whole earth is now completely comprised of Anthropogenic biomes (Ellis and Ramankutty 2008; Ellis *et al.* 2013). Temperate grassy woodlands around the globe persist in a continuum between an almost natural state and highly modified or cultural (Manning *et al.* 2006).

As discussed earlier, the anthropogenic use of European steppe environments for pastoral activities at the end of the Pleistocene may have preserved the structural formation into modern times Germany (Vera 2000; Pokorný *et al.* 2015). Agriculture and grazing prevented broadleaf forests from colonising the landscape as the climate warmed in the early Holocene (Pokorný *et al.* 2015) although the importance of wild herbivores in maintaining vegetation structure is much debated (Vera 2000; Birks 2005; Kuneš *et al*. 2015). Prehistoric humans throughout Europe created landscapes which mimicked natural forest-steppe

formations, preserving pasture for their domesticated herbivore stock to graze and maintaining trees for the harvest of fruits and fodder (Jørgensen and Quelch 2014). Fire was also an important land management tool for these early farmers (Kuneš *et al*. 2008; Pokorný *et al.* 2015). These landscapes can be termed cultural steppe or semi-natural grasslands (Pokorný *et al.* 2015).

The oak temperate grassy woodlands of North America have been occupied by humans for 12,000 years and it is understood that indigenous land management systems helped to maintain the open formation of savannas and woodlands when climate would have supported denser vegetation (Batek *et al.* 1999; Brewer and Vankat 2004). The temperate grassy woodlands of Australia were occupied and managed by indigenous people for 30–40,000 years. Australian Aboriginal people hunted kangaroo and other macropods in open temperate grassy woodlands (Bowman 1998). Many plant food resources were also found exclusively in open woodlands. Some researchers assert that temperate grassy woodlands of Australia are cultural landscapes (Gammage 2008, 2011) while others suggest that climate and soils have been equally important in maintaining the structure of woodlands (Fensham 1989). The impacts of Australian Aboriginal landscape management are difficult to determine because fire has been important on the continent since the Cainozoic and the flora is well adapted to fire (Bowman *et al.* 2011).

Some successful agroecosystems in forgiving environments superficially resemble the natural systems they replaced (Ewel 1999). The cultural woodlands of Europe are mostly synthetic and have been developed into sophisticated silvopastoral systems. For example, the temperate grassy woodlands (dehesa) of southern Spain has been used for agricultural production since the Middle Ages. Humans have preserved or created a landscape that is high in biodiversity and ecological complexity comprising species useful to humans (Joffre *et al.* 1999). On the other hand, temperate grassy woodlands in North America and Australia, are likely to be cultural artefacts but these have been overlayed with impacts of more recent European culture creating a complex conservation conundrum. The conservation status of many cultural temperate grassy woodlands is perilous as they are threatened by overuse, clearing and conversion to cropping or threatened by abandonment of long-standing management techniques and subsequent thinning or thickening of woody vegetation. Those regions that have a longer history of European settlement have

more synthetic, cultural temperate grassy woodland vegetation types, which are dependent on anthropogenic management.

Temperate grassy woodland regions

The following section describes temperate grassy woodland vegetation from various locations around the world. Large areas of temperate grassy woodland exist throughout the Mediterranean Basin, eastern Europe, Greece Turkey and the Middle East. A very small area of temperate grassy woodland can be found in Tajikistan. Cool temperate steppe-woodland and temperate woodland areas are found in Mongolia (Liu *et al*. 2000) and China (Liu *et al*. 2013). In North America, two distinct temperate grassy woodland areas are found, those on the west coast in a Mediterranean climate (California) and those which form the prairie/forest ecotone in the Midwest states. In South America, small areas of temperate grassy woodland are found in Chile, although these may have been degraded from other vegetation types (Mooney *et al.* 1970). Also in South America, temperate grassy woodlands form an ecotone between pampas and low forest in Argentina (Guida Johnson and Zuleta 2013). Temperate grassy woodlands are found in Australia, on both the west and east coasts; I will explore these more fully below. As described earlier, terminology discussing temperate grassy woodlands in the literature is variable and inconsistent. I discuss a subset of these temperate grassy woodlands below using local nomenclature based on published research, all of which have been influenced by European-style land management methods throughout their history.

Europe

Wood-pasture – Cultural temperate grassy woodlands of Europe include a range of silvopastoral systems (Bergmeier *et al.* 2010). They are most commonly found in Mediterranean countries and eastern Europe, particularly Spain, Portugal, France and Romania (Plieninger *et al.* 2015). Tree cover can be very low (>5%) and the ground layer is pasture or grassland with clear evidence of grazing (Plieninger *et al.* 2015). Large populations of 'ancient' trees are found in these managed ecosystems which provide hollows and habitat for fauna (Hartel *et al.* 2013). Often the trees within wood-pastures are coppiced or pollarded (Bergmeier *et al.* 2010), the landscape may also be managed for grass cutting, timber, charcoal, bee keeping and livestock (Bergmeier *et al.* 2010). Wood-pastures possess productive, heterogenous structural complexity and support high levels of biodiversity within this complexity (Díaz *et al.* 2013). Current management

systems may resemble the natural drivers of the pre-human environment which was probably a dynamic mosaic of trees and grass with large herbivore grazers. In regions that are modernising, wood-pastures are threatened by both agricultural intensification and abandonment of traditional farming methods (Plieninger *et al.* 2015).

Dehesa and montado of Spain and Portugal –These temperate grassy woodlands have been managed for agricultural productivity for at least 1000 years (Stevenson and Harrison 1992; Joffre *et al.* 1999). These anthropogenic woodlands are a noteworthy example of a landscape managed for production and conservation (Olea and San Miguel-Ayanz 2006). Seasonal grazing plays an important role in maintenance of Dehesa. Regeneration of trees is higher where there is transhumant grazing rather than permanent grazing (Carmona *et al.* 2013). Shifting grazing patterns allow for phases of tree and shrub regeneration followed by opening of woodlands when grazing returns, probably mimicking the dynamism of intermitted disturbances including grazing by large herbivores .Today, crop farming and grazing by goats or cropping provide disturbance which prevents shrubs from encroaching (Olea and San Miguel-Ayanz 2006).

North America

California oak woodlands – Modern agriculture and urban development patterns in California correspond closely to the original distribution of grasslands and oak woodlands (Murphy and Ehrlich 1989). Most of the Californian woodlands have been transformed and most remnants persist on private property within an agricultural matrix (Bolsinger 1988; Taft 1997). The few remaining stands of oak woodlands and savanna in California are degraded due to recruitment failure, invasion of exotic species, timber harvesting and disease (Bolsinger 1988; Sork *et al.* 2002; McPherson *et al.* 2005). Very little discussion in the literature exists regarding the understorey composition of Californian woodlands, but many of the species in grasslands are exotics.

The pre-European disturbance regimes of oak woodlands are uncertain and experimental evidence is often contradictory. Understorey species composition appears to be more affected by interannual weather patterns than by seasonal sheep grazing (Bartolome and McClaran 1992). Juvenile *Quercus douglasii* can reshoot after fire (Swiecki and Bernhardt 2001). Despite suggestions based on dendrochronology and fire-

scars that fire created a regeneration pulse of *Q. douglasii* (McClaran and Bartolome 1989), Swiecki and Bernhardt (2001) found no evidence to support this.

Midwest oak savanna – It is estimated that temperate grassy woodlands (tallgrass oak savanna) once covered 12 million ha in the Midwest of USA and occupied a transition zone between forests and prairie (Nuzzo 1986). Less than 1% of the former range persists, most has been converted to cropland and pasture (Rhemtulla *et al.* 2007).

Disturbance such as fire is essential for the maintenance of Midwest temperate grassy woodland (Penfound 1962; Dey and Kabrick 2015). Encroachment of shrubs suppresses growth of dominant overstorey species (*Quercus alba*) in Midwest oak temperate grassy woodlands (Brudvig *et al.* 2011) and transitions to a later successional forest types (van de Gevel and Ruffner 1964). Burning by Native Americans enabled woodlands to persist, despite changes in temperature and precipitation from 5000 BP, until modern times (Batek *et al.* 1999; Brewer and Vankat 2004). In the absence of burning, drought and livestock grazing help to maintain woodland structure. However, in the absence of fire the ground layer composition will decrease in herbaceous species diversity (Bacone *et al.* 2007).

Australia

Temperate grassy woodland dominated by *Eucalyptus* species – Temperate grassy woodlands in Australia are widespread and form a transition zone between higher rainfall forests and arid grass or shrublands. These grassy ecosystems stretch from Queensland through New South Wales and Victoria to eastern South Australila. They are also found in lowland areas of Tasmania and the southwest corner of Western Australia (Yates and Hobbs 1997a; Lunt *et al*. 2012). Temperate grassy woodlands have experienced the greatest declines of all vegetation types in Australia (Department of the Environment and Water Resources 2007). Since European settlement, more than 47 million hectares of eucalypt temperate grassy woodland have been cleared from southeast and south west Australia (Booth *et al.* 2015) due to agricultural expansion. Temperate grassy woodlands on flat, relatively fertile soils, particularly those near rivers, have suffered the greatest losses. Remnants of temperate grassy woodlands persist in a matrix of agricultural land and many

have ground layers much transformed from their native state by exotic weeds and pasture species (Yates and Hobbs 1997a).

The pre-European floristic composition of the ground layer is little known because changes for grazing occurred so rapidly after European settlement (Fensham 1989; Prober 1996). The resultant mix of grasses and forbs are a subset of the original vegetation that is more tolerant to European style disturbances (Wilcove *et al.* 1986; Lunt and Spooner 2005). Despite these changes, the ground layer remains highly diverse and is comprised of tussock grasses with forbs in the matrix and very few shrubs. Temperate grassy woodlands, especially those dominated by the C_4 grass *Themeda triandra*, require active management to maintain their biological and structural values. It is believed that Aboriginal people managed woodlands throughout Australia with frequent burning but direct evidence of this is mostly lost to history because Aboriginal groups in temperate areas of Australia were rapidly disenfranchised (Jones 1969; Bliege Bird *et al.* 2008).

Experimental data has revealed that *Themeda* dominated temperate grassy woodlands require burning every three to five years to ensure the ground storey does not become a monospecific stand of grass (Stuwe and Parsons 1977; Gilfedder and Kirkpatrick 1994; Zacharek *et al.* 1997). By contrast, *Poa*-dominated sites that remained unburned for over 60 years retained high forb abundance (Lunt *et al*. 2012). Forb abundance in these *Poa* sites declined if burned every two years (Lunt *et al*. 2012). The season of burning can be highly influential in the persistence of some *Poa* species in temperate grassy woodlands, short rotation spring burns appear to benefit the persistence of *Poa* and particularly favours resprouting species (Department of Sustainability and Environment 2003). Temperate grassy woodlands can also become invaded by native shrubs in the absence of fire (Watson and Morris 2006). Burning can, however, also increase the abundance of exotic species (Prober *et al.* 2016). Ideal fire return frequencies are still debated; recent analysis suggests that in eucalypt temperate grassy woodlands the typical fire return interval is broad, ranging from 12– 150 years and usually occurs in summer (Cheal 2010; Murphy *et al.* 2013). Furthermore, these fires are usually low in intensity 100 – 1000 kW m^{-1} (Murphy *et al.* 2013).

Climatic conditions within the temperate zone also influence fire's effects on the ground layer. Dead grass biomass accumulates rapidly in more mesic woodlands (Morgan and Lunt 1999, Prober et al 2007) but in

arid woodlands grass biomass does not seem to accumulate but rots or blows away rather quickly (Conway 2000). Fire regulates grass biomass in temperate grassy woodlands, but grass also regulates fire. In wet years with ample grass growth large fires are more likely (Hodgkinson and Harrington 1985).

In many temperate grassy woodland regions, the overstorey *Eucalyptus* species fail to recruit and widespread premature death of eucalypts is seen. In temperate grassy woodlands, recruitment only occurs after a major disturbance such as fire, flood or drought which is followed by above average rainfall in the first summer after germination (Burrows *et al.* 1990). This combination of events is rare in a naturally functioning landscape. In a modified landscape, where agriculture and anthropogenic climate change exert strong influence, these events are even rarer (Yates and Hobbs 1997b). In addition, some regions are witnessing the phenomenon of 'rural tree decline' whereby overstorey trees die prematurely due to a complex combination of biological changes including removal of native species, livestock grazing, introduction of pasture species and soil fertilisation (Close and Davidson 2004). These changes along with a rapidly changing climate imperil remnants of native vegetation.

Land use – threats and responses

Threats to temperate grassy woodlands are challenging for governments, NGOs and landowners globally who need to develop policy and practices that balance development with conservation needs, all within naturally dynamic vegetation complexes. Regions containing temperate grassy woodlands are often privately owned and heavily fragmented for farming enterprises. Growing human populations and technological developments mean that agricultural threats continually expand and intensify. Government policy makers recognise that agricultural production must expand to satisfy the needs of growing populations, and that biodiversity conservation is also valued in the same regions (Bardsley and Thomas 2006; Clement *et al.* 2017).

The needs of production and conservation can appear incompatible but attempts have been made to confront these issues in the '*land sparing, land sharing'* debate (Fischer *et al.* 2014). While some have argued that increasing the yield of existing farmland will reduce the demand for new land thus leading to *sparing land* for biodiversity within the productive landscape (Waggoner 1995), others suggest that intensive agriculture will continue to expand regardless, requiring improved governance to ensure land for

nature is preserved (Angelsea and Kaimowitz 2001; Macedo *et al.* 2012). *Land sharing,* on the other hand, proposes that land may be shared between farming and nature in 'wildlife-friendly' farming but possibly at the expense of agricultural yield (Green *et al.* 2005). Traditional silvopastoral farming systems within Europe combine economically important tree species with perennial pasture species, mixed crops and livestock grazing, and come very close to the concepts of *land sharing* (Fischer *et al.* 2011). Ecoagriculture landscapes borrow from traditional European integrated landscape management techniques and adapt these to explicitly promote environmental conservation (Scherr and McNeely 2008). The focus of policy makers has shifted away from conserving singles species to preserving whole ecosystems, consequently, non-target elements are preserved (Bardsley 2008). As well as non-target species these include ecosystem services such as nutrient cycling (Scherr and McNeely 2008), pollination services (Boreux *et al.* 2013) or abiotic components such as riverine systems (Beechie *et al.* 2010).

Tasmanian context

The Midlands of Tasmania contain the southernmost temperate grassy woodlands of Australia (Figure 2). These temperate grassy woodlands form a zone transition between lowland grasslands and dry eucalypt forests. The Midlands occupy a dry, lowland area in a rain shadow created by the Central Plateau making the region the driest of Tasmania. Annual rainfall is 390 – 630 mm, evenly distributed through the year. The climate is classified as temperate with warm summers (Peel *et al.* 2007).

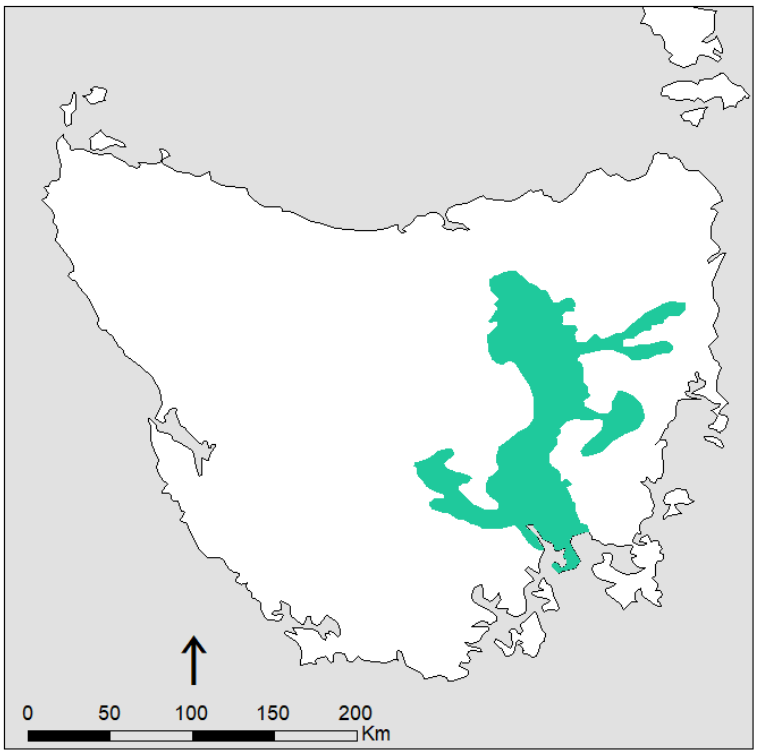

Figure 2. Areas containing lowland temperate grassy woodland in Tasmania (green). At the time of European arrival, approximately 1.25 million ha contained a mosaic of temperate grassy woodlands and grasslands, much of this is now cleared for agriculture. Adapted from Kirkpatrick and Gilfedder (2000).

Aboriginal people migrated to Tasmania some 30,000 years ago and did not have contact with Europeans until indirect contact with Abel Tasman when he mapped part of the island in the 1640s (Boyce 2008) then cultural contact from 1770s during a phase of British and French exploration (Evans 2012). Tasmania has been isolated from mainland Australia for about 12,000 years after sea levels rose at the end of the last glacial period (Hope 1999). In 1803 the first European settlement was created in Tasmania. Europeans rapidly settled the island so that by the 1830s most of the good arable land, comprising both grassland and temperate grassy woodland, through the Midlands corridor between Launceston and Hobart was allocated to European settlers (Plomley 1966; Easteal 1971). Europeans and Aboriginal people clashed, often violently (Boyce 2008; Ryan 2012). Successive colonial governments attempted to remove all tribal Aborigines from the mainland of Tasmania to Flinders Island (Madley 2012). Eventually, forty-seven people were removed from Flinders to Putalina (Oyster Cove) just south of Hobart. A number of women and children survivied and their children form the basis of the present day Palawa (Aboriginal) population (Ryan 2012).

Due to hostile relations between Aboriginal people and the first Europeans, knowledge about the pre-European vegetation and traditional land management is incomplete. Moreover, the speed at which the temperate grassy woodlands of the Midlands were overtaken by European agriculture means the vegetation changed rapidly and these changes were not documented. Despite this, the structure of temperate grassy woodland vegetation in the Midlands has been reconstructed using historical sources and floristic surveys (Fensham 1989) but uncertainties regarding the original state of the vegetation and its maintenance regime persist.

Throughout the Midlands substantial areas have lost overstorey trees due to rural tree decline (Neyland 1999; Kirkpatrick *et al.* 2000; Close and Davidson 2004). Isolated trees within paddocks grazed by sheep have died and there is little recruitment in areas where trees do persist. The temperate grassy woodlands throughout the Midlands have deviated so far from their historical state that most have already transitioned to a degraded alternative stable state. Conservation reserves have been created to protect small remnants of temperate grassy woodlands. However, the landscape is mostly privately-owned so the area for public conservation is very small. In this privately-owned landscape many landowners have enacted conservation efforts to preserve temperate grassy woodlands on their land.

Outline of thesis

This thesis examines recent historical change (600 years BP to the present) and the likely future trajectory of the temperate grassy woodlands of Tasmania within the context of global temperate grassy woodland communities and landscapes. Field studies and geographical analyses were undertaken to explore three areas related to the influence of human use and management on the composition, structure and persistence of this temperate grassy woodland type. Throughout this thesis, various terminology is used in the individual chapters to refer to the 'grassy woodlands' of the Tasmanian Midlands.

Chapter 1

I analyse sediment cores from lakes in the Tasmanian Midlands to identify

1.1 Changes in vegetation patterns after the arrival of European settlers

1.2 Changes in fire regimes after the arrival of European settlers

1.3 Pre-European Aboriginal land use

Chapter 2

By analysing remotely sensed data for the Tasmanian Midlands I

2.1 Compare the rate of landscape clearing during the periods 1945-2010 and 1788-1945

2.2 Quantify the amount of carbon lost from the landscape during the period 1945-2010

2.3 Determine the extent of revegetation required to replace the carbon lost through vegetation clearance for agriculture and mitigate the projected effects of climate change

Chapter 3

I use demographic analysis of replicated vegetation plots to determine whether

3.1 There are differences between the effectiveness of public and private reserves in protecting survival and recruitment of over storey tree species

3.2 Private conservation reserves can effectively preserve over storey tree species and promote recruitment

3.3 Prior land use history influences success of reserves in protecting survival and recruitment of over storey tree species

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Chapter 1

ire regime and vegetation change in the transition from Aboriginal to European land management in a Tasmanian eucalypt savanna

Louise M Romanin, Feli Hopf, Simon G Haberle, David M J S Bowman

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Fire regime and vegetation change in the transition from Aboriginal to European land management in a Tasmanian eucalypt savanna

Louise M. Romanin[A,C], *Feli Hopf*[B], *Simon G. Haberle*[B] *and David M. J. S. Bowman*[A]

[A]School of Biological Sciences, University of Tasmania, Private Bag 55, Hobart, Tas. 7001, Australia.
[B]ANU College of Asia and the Pacific, Australian National University, Canberra, ACT 0200, Australia.
[C]Corresponding author. Email: Louise.Romanin@utas.edu.au

Abstract. Using pollen and charcoal analysis we examined how vegetation and fire regimes have changed over the last 600 years in the Midlands of Tasmania. Sediment cores from seven lagoons were sampled, with a chronology developed at one site (Diprose Lagoon) using ^{210}Pb and ^{14}C dating. Statistical contrasts of six cores where *Pinus* served as a marker of European settlement in the early 19th Century and showed significant changes in pollen composition following settlement with (a) influx of ruderal exotic taxa including *Plantago lanceolata* L., Brassicaceae, Asteraceae (Liguliflorae) and *Rumex*, (b) increase in pollen of the aquatics *Myriophyllum* spp. and Cyperaceae, (c) a decline in native herbaceous pollen taxa, including Chenopodiaceae and Asteraceae (Tubuliflorae) and (d) a decline in *Allocasuarina* and an initial decline and then increase of Poaceae. The presence of Asteraceae (Liguliflorae) in the pre-European period suggests that an important root vegetable *Microseris lanceolata* (Walp.) Sch.Bip. may have been abundant. Charcoal deposition was low in the pre-European period and significantly increased immediately after European arrival. Collectively, these changes suggest substantial ecological impacts following European settlement including cessation of Aboriginal traditions of fire management, a shift in hydrological conditions from open water lagoons to more ephemeral herb covered lagoons, and increased diversity of alien herbaceous species following pasture establishment.

Additional keywords: Aboriginal fire management, grassland, grassy woodland historical ecology, landscape ecology, macro-charcoal, palynology.

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Introduction

The transition from Aboriginal to European management is a critical period in the history of Australian ecosystems. European colonisation of Australia, which commenced in 1788, resulted in the introduction of new plants, animals and microorganisms, some of which initiated a wave of native plant and animal extinctions (MacPhee and Flemming 1999; Woinarski *et al*. 2015). Aboriginal people were removed from their traditional lands causing the loss of ancient socio-ecological systems, and native vegetation was modified for farmland, urban areas and mines (Fensham 1989; Lunt 1991). Particularly hard hit were temperate environments, especially those dominated by native grasslands and woodlands with a grassy understorey that collectively form a savanna biome. These regions were ideal for early pastoral settlement, which lead to rapid changes in land management (Benson and Redpath 1997). The oldest agricultural landscapes in Australia are woodlands on the Cumberland Plain to the west of Sydney, settled in 1791, and the Midlands of Tasmania settled from the early 1820s (Phillip 1892; Morgan 1992). The conversion of temperate grassland and woodland ecosystems, which we collectively describe as 'temperate savanna', has been almost complete with less than 20% of these ecosystems remaining on mainland Australia and Tasmania (Kirkpatrick *et al*. 1988; Fischer *et al*. 2009).

There are sparse data on Aboriginal land use practices in temperate savannas given that these ecosystems were impacted so early in the colonial historical of Australia. Archaeological evidence has illuminated patterns of Aboriginal land occupancy and there are early colonial reports of Aboriginals burning the landscape; however, the ecological consequences and frequency of burning is unclear (Kee 1990; Brown 1991). Aboriginal land management continues with relatively little disruption in tropical Australian savannas but there is uncertainty about the applicability of these contemporary management practices in to temperate Australian systems (Bowman 1998; Russell-Smith *et al*. 2013). For these reasons, prehistorical reconstructions of Aboriginal land management regimes are of prime importance in these temperate ecosystems.

Broadly, there are two different approaches to reconstruction of past environments: environmental history, stemming from

the humanities; and historical ecology from the sciences (Bowman 2002). The former relies on interpretation of historical documents and images (Ryan *et al*. 1995; Bowman 2002; Butzer and Helgren 2005; Mactaggart *et al*. 2007; Gammage 2008) and the latter, environmental reconstructions using a range of proxies, the most important being dendrochronology (Banks 1982; von Platen *et al*. 2011) and pollen and charcoal in sediments (Swetnam *et al*. 1999; Whitlock and Larsen 2001; Turner and Plater 2004; Higuera *et al*. 2005; Black *et al*. 2007). These approaches are not mutually exclusive, indeed sometimes they motivate and inform each other, and can be effectively merged to provide more robust reconstructions of vegetation cover (Fensham 1989; Batek *et al*. 1999; Benson and Howell 2002; Lunt 2002).

In temperate Australia there is a suite of direct scientific analysis of the transition from Aboriginal to European management (summarised by Dodson and Mooney 2002) but in temperate savanna landscapes there has been a far greater reliance on the analysis and interpretation of historical records (Fensham 1989; Thomas 1994; Griffiths 2002; Lunt 2002; Gammage 2008, 2011). These qualitative studies have been influential on contemporary management practices, especially tree clearing in rural landscapes and bushfire management (Rolls 1981; Benson and Redpath 1997; Jurskis 2000; Mooney *et al*. 2007; Attiwill and Adams 2013). A particularly prominent view is that the amount of landscape burning declined abruptly following colonisation, resulting in a thickening of landscapes that were formerly much more open (Rolls 1981; Jurskis 2000; Franco and Morgan 2007; Gammage 2011). Despite their popular appeal, there has been limited independent verification using robust environmental proxies leading to ongoing debate between scientists and historians about landscape history (Benson and Redpath 1997; Flannery 1997; Jurskis 2000; Bowman 2001).

The Midlands of Tasmania are important in discussions about the nature of landscape changes that followed European settlement. The temperate savannas, which supported high densities of kangaroos and an endemic and now extinct emu, are assumed to have been maintained by frequent landscape burning (Jones 1969; Duncan 1990; Bowman 1998; Jackson 1999; Gammage 2008), a practice that is likely to reach back to the beginning of Aboriginal colonisation some 35 000 years ago (Colhoun and Shimeld 2012; O'Connell and Allen 2015). The open vegetation proved ideal for sheep grazing, so the grassy lowlands of the Midlands were rapidly allocated to free settlers and by 1830, Aboriginal people were completely removed from the area (Fensham 1989; Morgan 1992; Benson and Redpath 1997). This transition resulted in tree clearance, establishment of exotic taxa and the transformation of a focal region of the indigenous economy (Ryan 2012; Prior *et al*. 2013; Romanin *et al*. 2015).

There is a diverse range of evidence to support the hypothesis that Aboriginal people used fire to create or maintain open landscapes in wetter regions of Tasmania (Ellis and Thomas 1988; Jackson 1999; Fletcher and Thomas 2010; Wood and Bowman 2012; Bowman *et al*. 2013). However, there is less evidence to support this hypothesis in the Midlands where there has been a great reliance on the veracity of early colonial paintings that depict vast savanna landscapes with open crown eucalypts (Duncan 1990; Kirkpatrick 2007; Gammage 2008). The accuracy of these paintings is questionable because they were executed with different motivations. Some artists were employed by the government to create immigration propaganda, which was picturesque and had a strong resemblance to English landscapes, some were trained as surveyors and produced highly accurate landscape representations, still others were artistically trained so used artistic licence to create aesthetically-pleasing scenes (Fensham 1989; Farag-Miller *et al*. 2013). The landscapes of Glover are often referred to as accurate pre-European depictions of the Midlands, his works were criticised by contemporaries for their 'hideous fidelity to nature' (Smith 1960; Fensham 1989). Nonetheless, he portrayed groups of Aboriginal people in landscapes free of European disturbance despite them being expatriated years previously, and independent geographic validation using surveying techniques demonstrates that Glover's landscape features are of low topographic fidelity (Farag-Miller *et al*. 2013). Considering these factors it is reasonable question his artworks' ecological and botanical fidelity as well.

The scientific evaluation of the environmental changes in the Midlands is limited to a dendrochronological study in the dry sclerophyll forest of the eastern tiers (von Platen *et al*. 2011), preliminary palaeoecological examinations of the long-term pollen and charcoal record in a Midlands lagoon (Sigleo and Colhoun 1981), an unpublished thesis looking at the pollen and charcoal record of an additional Midlands lagoon (Jones 2008) and inferences from current demographic structure and open branching habit of old woodland trees (Duncan 1990; Kirkpatrick 2007; Gammage 2008). These studies together suggest that Aboriginal fire was infrequent or low in severity (von Platen *et al*. 2011) and the dominant vegetation was eucalypt savanna with a substantial *Allocasuarina* component (Sigleo and Colhoun 1981; Jones 2008) before European settlement. Immediately after Europeans arrived, fire frequency, as recorded in fire scars, decreased dramatically but increased again in frequency between 1850 and 1980, after 1989 there were few fires recorded (von Platen *et al*. 2011). The single analysis of macro-charcoal in the Midlands showed sparse levels in both the pre- and post-European periods; however, micro-charcoal seems to have been more abundant pre-settlement (Jones 2008). Pictorial evidence used by Duncan (1990) and Gammage (2008) suggest that the elimination of Aboriginal land management resulted in increased density of trees in uncleared fragments, with widely spaced, wide-canopied trees being replaced by narrow crowned, pole saplings and younger trees.

In this study we sampled sediments from seven lagoons and used pollen and charcoal analysis to examine how vegetation and fire regimes at a landscape-level have changed following European colonisation of the temperate savannas of the Midlands of Tasmania. This is the most extensive sampling of this region to date. According to previous research we expect to see a sharp decrease in fire activity post settlement and then a subsequent increase. Trends in the floristic composition of post settlement vegetation are expected to include a mixed signal of increased ruderals and (pasture) grasses and non-native trees, and a loss of native species, particularly herbs and fire sensitive woody taxa including *Allocasuarina*.

Materials and methods

Geographic context

Our study locus was the Midlands of Tasmania – a region that is characterised by fertile river valleys and lateritic plains lying between the Central Plateau to the west and the Eastern Tiers to the east (Fensham and Kirkpatrick 1989; Doyle 1993). The region is in a rain shadow (Fig. 1*a*) and is the driest part of the island with rainfall between 397 and 626 mm annually, evenly distributed throughout the year (Fig. 1*b*). Average maximum temperatures range between 9 and 11°C in winter and 21 and 24°C in summer. The regional climate is classified as temperate with warm summer according to Köppen-Geiger classification (Peel *et al*. 2007). Frosts can occur during any month and the average number of frost days across the region is between 75 and 150 per year (Bureau of Meteorology 2008).

The original vegetation of the area based on historical reconstructions was a mosaic of lowland grasslands and grassy eucalypt woodland dominated by *Eucalyptus viminalis* Labill., *Eucalyptus pauciflora* Sieber ex Spreng. and *Eucalyptus amygdalina* Labill. with understorey trees such as *Allocasuarina verticillata* (Lam.) L.A.S.Johnson, *Acacia dealbata* Link and *Banksia marginata* Cav. and a tussock grassland dominated by *Poa labillardieri* Steud. and *Themeda triandra* Forssk. (Fig. 1*c*) (Fensham 1989; Fensham and Kirkpatrick 1989). Approximately 37% of the region remains under natural vegetation, most of which is highly fragmented (Norton and Lacey 2012) due to extensive clearing for pasture and crops (Fig. 1*d*) that occurred over the last ~200 years of European settlement. Small wetlands with varying levels of salinity occur throughout the region (David and Browne 1950; Buckney and Tyler 1976; Kirkpatrick and Harwood 1983),

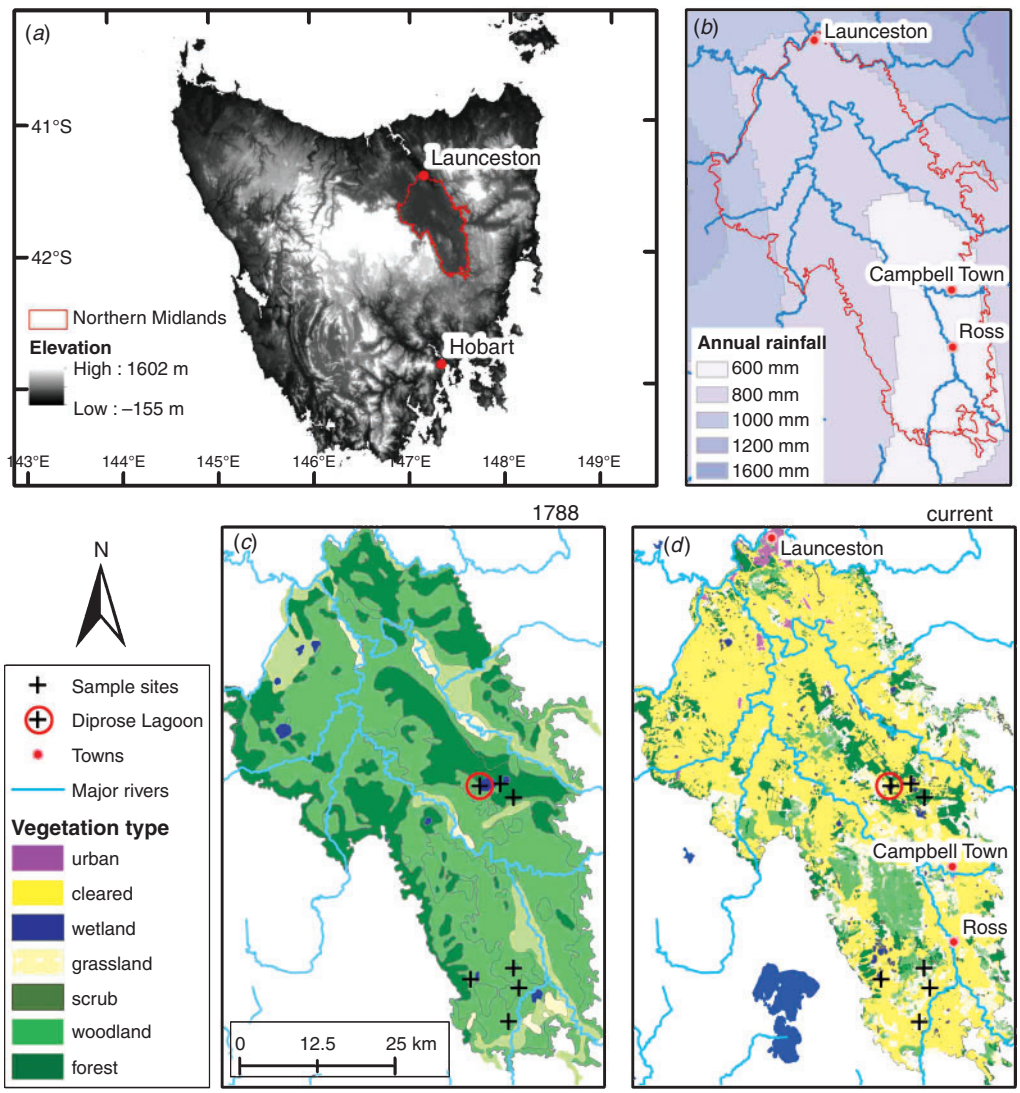

Fig. 1. Geographic context of the study area showing (*a*) elevation across Tasmania with the study area outlined in red; (*b*) annual rainfall across the study area which ranges from 600 to 1000 mm annually; (*c*) a reconstruction of 1788 vegetation patterns (adapted from Fensham 1989) and (*d*) current vegetation patterns (adapted from TASVEG 2.0; Department of Primary Industries and Water 2009) with locations of sampling sites marked as black crosses in both the 1788 and current vegetation maps. The core from Diprose Lagoon that was ^{210}Pb and ^{14}C dated to obtain calibrated chronology is circled in red.

supporting sedge and rushlands dominated by a suite of genera including *Juncus*, *Baumea*, *Carex*, *Lepidosperma* and *Phragmites* and herblands with ephemeral aquatic plants such as *Myriophyllum* spp. and *Triglochin* spp. where open water is present. The most saline wetlands support salt marsh communities including *Chenopodium* spp. (Kirkpatrick and Glasby 1981).

Sediment sampling

Sediment cores were collected from seven lagoons along a ~40 km long, north–south transect spanning the study area (Fig. 1*c*, *d*). The lagoons varied in condition and aquatic vegetation therefore a variety of methods were used to collect sediment samples; sample resolution was necessarily low at one site due to the dryness of the sediments (Table 1). A d-section corer was used where sediments were soft enough for corer penetration. A hammer-driven polycarbonate piston corer was used where sediments were dominated by stiff clays. All cores were wrapped in plastic and stored in PVC tubes. They were kept cool and subsequently subsampled for macro-charcoal and pollen analysis.

Charcoal and pollen analysis

Macro-charcoal particles (>125 µm) are likely to be derived from local fire events (Whitlock and Larsen 2001; Duffin *et al.* 2008). To prepare samples for macro-charcoal analysis, a subsample of 1.25 cm^3 of material from each contiguous 0.5 cm increment was extracted. Subsamples with high clay content were deflocculated in Calgon solution for 2–3 days, after which samples were rinsed gently with water. Charcoal subsamples were then treated with bleach for at least 24 h to remove the pigment from organic matter and aid in identifying charcoal (Black *et al.* 2007). Bleached samples were gently washed through a 125 µm sieve to separate macro-charcoal from organic matter and finer particles. Total macro-charcoal particles were counted under a low power stereo-microscope.

Broad vegetation patterns over time were examined through pollen analysis. Sediment records were sampled at 2 cm intervals; 1.25 cm^3 subsamples of these were analysed at Australian National University (ANU) using standard preparation and counting techniques by Bennett and Willis (2001). Pollen identification and nomenclature follows species lists included by Zacharek *et al.* (1997), plant surveys at Tom Gibson Nature Reserve (Parks and Wildlife Service Tasmania 2006) and reference collections held at ANU (http://apsa.anu.edu.au, accessed 5 May 2014). *Eucalyptus* and *Allocasuarina* type pollen is assigned based on current vegetation patterns. Terrestrial or dryland pollen counts (including fern spores but excluding aquatic taxa) were expressed as percent pollen of each sample and used in statistical analyses where: (a) taxa that occurred in less than four samples per core or made up less than 1% of the total were excluded from analysis ($n = 17$); (b) all *Rumex* types were treated as one taxon as distinguishing between native and exotic *Rumex* taxa that coexist in Tasmania is problematic; (c) indeterminate pollen grains were also excluded from analysis.

Sediment chronology

Diprose Lagoon was selected for ^{210}Pb and ^{14}C dating at Australian Nuclear Science and Technology Organisation (ANSTO) (Lucas Heights, NSW, Australia). The upper 12 cm of the core was analysed for ^{210}Pb activity, and the constant rate of supply (CRS) model was used to develop a chronology for Diprose Lagoon (Oldfield and Appleby 1984). The CRS model assumes a constant flux of unsupported ^{210}Pb to the surface sediments through time (Appleby and Oldfield 1978; Binford 1990). This model is suitable for many temperate-zone lakes where ^{210}Pb activity has been diluted by recent high sediment accumulation rates (Binford 1990) and is appropriate in this

Table 1. Sampling details of the seven lagoons in the Midlands of Tasmania

The location and landscape setting, sampling methods employed for extracting sediment and their total length of each core, sampling resolution is summarised for each site. The first occurrence of *Pinus* is also noted

Lagoon name	Location	Landscape setting	Sampling method	Length of core	Sampling resolution	*Pinus* 1st record
Diprose Lagoon	41°48′25.26″S, 147°22′16.26″E	Agricultural land, *Eucalyptus amygdalina* woodland	Universal core sampler	21.5 cm	2 cm (pollen), 0.5 cm (charcoal)	10 cm
Smiths Lagoon	41°49′22.95″S, 147°26′11.64″E	*Eucalyptus amygdalina* woodland	Shovel excavation	14 cm	2 cm (pollen), 0.5 cm (charcoal)	10 cm
Near Lagoon	42° 4′11.85″S, 147°26′15.83″E	*Themeda* and *Poa* grasslands, *Eucalyptus viminalis* grassy woodlands and *Eucalyptus pauciflora* woodland	Auger	36 cm	2 cm (pollen), 2 cm (charcoal)	22 cm
White Lagoon	42° 5′55.92″S, 147°26′55.12″E	*Themeda triandra* grassland *E. viminalis* woodland	Universal core sampler	26 cm	2 cm (pollen), 0.5 cm (charcoal)	10 cm
Bells Lagoon	42° 5′10.21″S, 147°21′14.89″E	Agricultural land, native lowland grassland complex, *E. viminalis* woodland	Universal core sampler	28 cm	2 cm (pollen), 0.5 cm (charcoal)	4 cm
Township Lagoon	42° 8′50.13″S, 147°25′,.36″E	Agricultural land, native lowland grassland complex	Universal core sampler	34 cm	2 cm (pollen), 0.5 cm (charcoal)	26 cm
Cleveland Lagoon	41°48′12.71″S, 147°24′38.16″E	Agricultural land, *E. amygdalina* and *E. viminalis* woodland	Shovel excavation	21 cm	2 cm (pollen), 0.5 cm (charcoal)	Throughout

landscape characterised by recent vegetation clearance and subsequent erosion (Sigleo and Colhoun 1982). To estimate the ages of the deeper sediments AMS radiocarbon (^{14}C) dating was used. Two samples were analysed, however, only that from 20 cm depth gave an age consistent with the ^{210}Pb chronology, whereas the sample at 15 cm gave an age that is best explained as contaminated with older carbon or otherwise unreliable. Age-depth modelling of the ^{210}Pb and ^{14}C chronology was performed using the CLAM package in R (R Development Core Team 2008; Blaauw 2010); a smoothed spline curve was fitted to the ^{210}Pb and ^{14}C dates. In the remaining six cores the occurrence of *Pinus* spp. was used as an unambiguous, albeit conservative, marker to divide into pre- and post-European periods (Mooney *et al*. 2001). One core (Cleveland Lagoon) was found to have *Pinus* throughout the entire core so was excluded from further analysis.

Data analysis

Changes in macro-charcoal and major terrestrial and aquatic pollen types were investigated for the dated core from Diprose Lagoon through graphical analysis and detrended correspondence analysis (DCA). To determine whether macro-charcoal had changed since the first appearance of *Pinus* spp. (i.e. pre- and post-European periods), all sites except Cleveland were combined, log-transformed, then analysed by a Mann–Whitney U test. Using the percentage pollen data for the six sediment cores, boxplots were generated to examine the distribution of pollen abundance in the pre- and post-European periods for the following ecological groups of taxa: (a) dry sclerophyll forest trees – *Allocasuarina* spp. and *Eucalyptus* spp.; (b) native herbaceous taxa – Poaceae, Asteraceae (Tubuliflorae) and Chenopodiaceae; and (c) exotic ruderal taxa – Brassicaceae, Asteraceae (Liguliflorae) and *Plantago lanceolata.* The difference in pollen percentage between the two periods for these ecological groups was modelled using generalised linear models with a quasibinomial distribution to account for the overdispersed proportion data. All analyses were performed using the R statistical software package (R Development Core Team 2008), ordinations were performed using the vegan package (Oksanen *et al*. 2015).

Results

Diprose Lagoon

The geochronology using ^{210}Pb and ^{14}C of the 22 cm Diprose Lagoon core indicates a continuous and surprisingly linear sediment record over the past ~600 years (Tables 2, 3). The lowest ^{210}Pb measurement at 12 cm depth coincides with European arrival in Tasmania (1803) (Fig. 2*a*). There are changes in the physical composition of the sediments with the post-European sediments being loamy, whereas the pre-European sediments are clay mixed with organic matter to 18 cm, after which clays are less enriched in organic matter. There is a corresponding strong decline in pollen preservation down the profile with a concentration of 3.2 pollen grains per cm^3 at the lowest depth (21.5 cm).

There were clear changes in floristic composition through the core, with a conspicuous decline in the abundance of the two dominant tree taxa *Eucalyptus* and *Allocasuarina* throughout the post-European period (Fig. 2*b*). At the time of settlement, *Eucalyptus* formed ~50% of the pollen assemblage falling to ~10% in the upper (modern) sediments. In the same period *Allocasuarina* declined from 15 to 4% (Fig. 2*b*). Poaceae (grass) pollen was the most plentiful herbaceous group, being relatively common (7–25%) in the pre-European period, but its abundance dropped immediately after European arrival (Fig. 2*c*). Since AD1990 Poaceae has become the most abundant (35%) in the terrestrial pollen record. Asteraceae (Tubuliflorae) or 'native daisy' pollen also showed a decline following European settlement from being the most abundant herbaceous taxon (25% of the pollen record) in the 14th century (Fig. 2*c*) declining to 1–5% of the terrestrial pollen in the 20th century. Chenopodiaceae first appeared in the record at around the time of European settlement, and has maintained low levels (~1%) throughout the modern period. Amongst the aquatic pollen, there is a striking transition from *Botryococcus* spp. to *Myriophyllum* spp. at around AD1940 (Fig. 2*d*). Cyperaceae pollen first appears at AD1870 and increases in abundance towards the surface. *Pinus* spp. also first occurs at around AD1870 reaching peak abundance at AD1960 and declining in modern sediments. Asteraceae (Liguliflorae) pollen is often used as indicator of the European period, but is not diagnostic here as there are native Tasmanian species within this pollen type including the important edible plant, *Microseris lanceolata* 'yam daisy', which may have formed part of the diet of Aboriginal people in the region (Gott and Murray 1982). Its presence in both the pre- (AD1630) and post-European sections of the core indicates there were native species in the region that were replaced by exotic taxa (Fig. 2*e*). A full pollen diagram is

Table 2. ^{210}Pb dating for Diprose Lagoon core from the in the Midlands of Tasmania

Dating was performed by Australian Nuclear Science and Technology Organisation (ANSTO). Depth of sample, level of radioactivity, and calculated age based on a constant rate of supply (CRS) model are supplied

Depth (cm below surface)	Total ^{210}Pb (Bq kg^{-1})	Mass accumulation rates (g cm^{-2} year^{-1})	Calculated CRS ages (years)
0–3	138 ± 6	0.091 ± 0.005	9 ± 3
3–4	139 ± 7	0.053 ± 0.004	26 ± 5
4–5	129 ± 6	0.043 ± 0.004	35 ± 6
5–6	109 ± 5	0.035 ± 0.003	47 ± 7
6–7	82 ± 4	0.028 ± 0.004	66 ± 8
7–8	53 ± 2	0.026 ± 0.005	88 ± 9
9–10	33 ± 2	0.025 ± 0.009	134 ± 12
11–12	23 ± 1	0.014 ± 0.012	192 ± 29

Table 3. ^{14}C AMS dates for Diprose Lagoon core in the Midlands of Tasmania

Depth of sample, δ13C of samples and calculated sample ages with 1δ error are provided

Depth (cm below surface)	δ(^{13}C) per mil	Conventional ^{14}C age ^{14}C year before present	1δ error
15 cm[A]	–30.3	1932	28
20 cm	–35.0	538	22

[A]Sample excluded from age–depth model due to suspected contamination of sample with older reworked carbon.

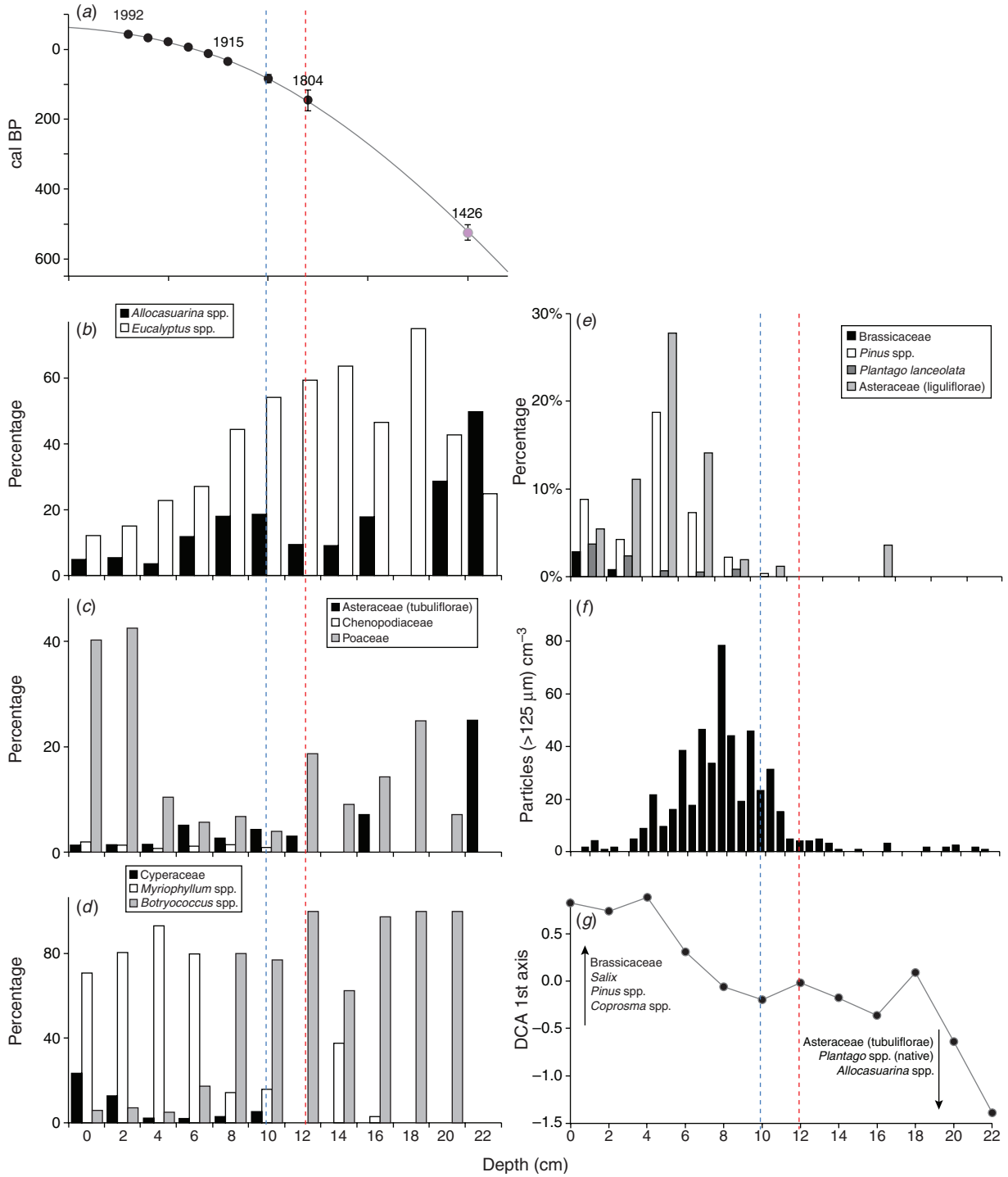

Fig. 2. Variation in pollen and charcoal in the dated core from Diprose Lagoon in the Midlands of Tasmania. (*a*) An age-depth model was developed using CLAM in R (Blaauw 2010) by fitting a smoothed spline curve to the ^{210}Pb (black) and ^{14}C (coloured purple) dates, estimated ages were converted to calendar years with 1950 as the baseline. The *x*-axis is depth in cm, with surface sediments at the left. The scale of the *y*-axis varies in each panel. The blue vertical line indicates the depth at which the first grain of *Pinus* pollen was found, the red vertical line indicates the approximate year that Europeans arrived in Tasmania; (*b*) percentage of the major dry forest tree taxa pollen, *Allocasuarina* spp. and *Eucalyptus* spp. (based on dryland pollen sum); (*c*) percentage of native herbaceous groups, Poaceae, Asteraceae (Tubuliflorae) and Chenopodiaceae (based on dryland pollen sum); (*d*) percentage of aquatic taxa, Cyperaceae, *Myriophyllum* spp. and *Botryococcus* spp. (based on the aquatic pollen sum excluding dryland taxa); (*e*) percentage of exotic indicator groups including the tree species *Pinus*, and the ruderal herbs, Brassicaceae, *Plantago lanceolata* and Asteraceae (Liguliflorae) (based on dryland pollen sum); (*f*) contiguous record of macro-charcoal (particles >125 microns with sample resolution of 0.5 cm); (*g*) the first axis of the DCA plotted against depth of the core, a steep slope of the axis indicates periods of rapid vegetation change. Pollen was analysed at 2 cm resolution.

included in Fig. S1, available as Supplementary Material to this paper.

Charcoal was present throughout the sediment record, though the uppermost sediments, after AD1990, have very low but fairly continuous macro-charcoal deposition. A major peak in macro-charcoal preserved in the sediments was found in the mid-19th and early 20th century (Fig. 2*f*). After the 1950s charcoal deposition dropped to near pre-European levels. In the pre-European period there is only a small amount of charcoal deposited, with gaps in the record.

The first axis of a DCA ordination of the terrestrial pollen taxa reflects the rate and direction of vegetation change following European settlement (Figs 2*g*, 3). In the early 20th century there is rapid floristic transition largely driven by the establishment of exotic taxa (Fig. 2*e*). The taxa that drive this transition are those with the strongest positive DCA scores and include *Coprosma* spp. as well as exotic taxa, Brassicaceae, *Salix* spp., *Pinus* spp. (Fig. 3). This transitional period also corresponds to the peak macro charcoal (Fig. 2*f*). In the earliest part of the record (AD1320–AD1530) there is also rapid taxonomic turnover that corresponds to the transition from *Allocasuarina* to *Eucalyptus* dominance (Fig. 2*b*). The native species that comprise the negative portion of the DCA first axis are Asteraceae (Tubuliflorae), *Plantago* spp. (native) and *Allocasuarina* spp. (Fig. 3).

Regional network

Total pollen preservation varied substantially between the wetlands. Township and Cleveland Lagoons had very good preservation throughout the length of the core. Diprose, White, Near and Smiths Lagoons had excellent pollen preservation in the upper sections of the sediment profile, but much poorer pollen preservation in the deepest sediments, particularly so for Smiths and, as noted previously, Diprose Lagoon. Bells Lagoon had high pollen preservation only in the surface sediment sample, the remainder of this core had poor preservation. Summaries of pollen and charcoal found at the six lagoons not discussed in detail are included in Fig. S2 and a list of all pollen and spore taxa recorded in this analysis is included in Table S1, available as Supplementary Material to this paper.

We used the first incidence of *Pinus* spp. pollen to approximate European settlement (Kodela and MacKillop 1988) in all of the cores except Cleveland Lagoon because it had *Pinus* pollen throughout, and overall pre- and post-European periods were examined. Among the remaining 6 cores *Pinus* constitutes 6% of the total terrestrial pollen with an interquartile range of 0.5–8%. In these cores the first appearance of *Pinus* varied from 4 to 26 cm depth, indicating different rates of sedimentation in the wetlands (Table 1). We used these six cores for statistical contrasts in pollen between the pre (– *Pinus*) and post (+ *Pinus*) European periods. For these cores there was no statistically significant change in the proportion of *Eucalyptus* pollen after the arrival of Europeans across the region ($P = 0.484$) (Fig. 4); however, there was a statistically significant decrease in *Allocasuarina* pollen ($P = 0.01$) (Fig. 4). In the deepest sections of four cores *Allocasuarina* pollen was at least as common as *Eucalyptus*. There were marked increases in Poaceae pollen abundance after settlement with Asteraceae (Tubuliflorae) and Chenopodiaceae pollen abundance

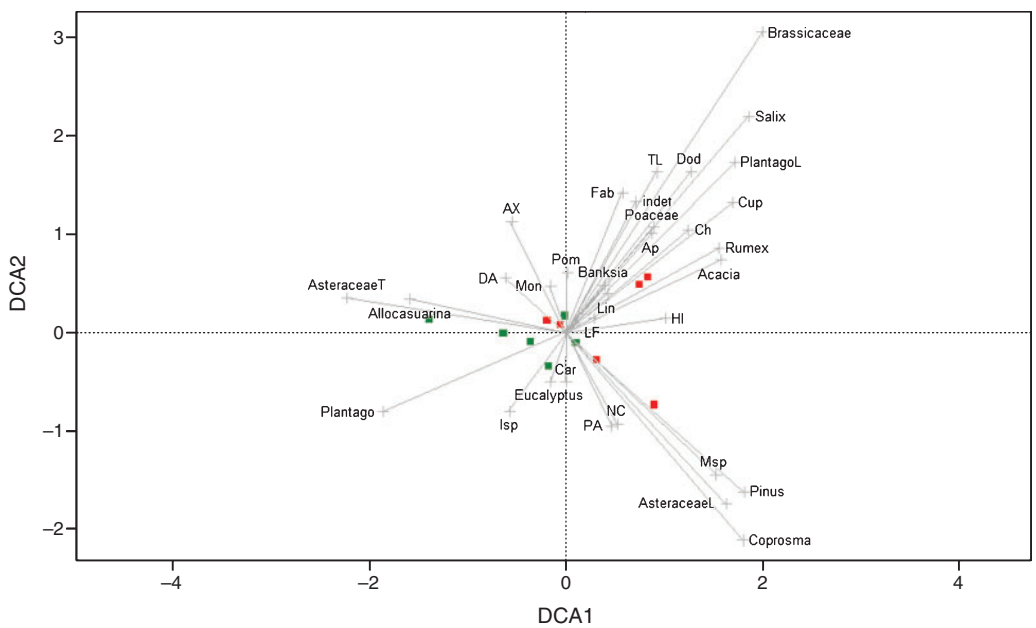

Fig. 3. Detrended correspondence analysis (DCA) of sediment record from Diprose Lagoon. Green squares indicate samples from the pre-European period (as determined by the absence of *Pinus* spp. pollen), red squares indicate samples from the post-European period. All the taxa with a strong influence on the first two axes are indicated where the following abbreviations are used: AP, Apiaceae; AsteraceaeL, Asteraceae (Liguliflorae); AsteraceaeT, Asteraceae (Tubuliflorae); AX, *Amperea xiphoclada*; Car, Caryophyllaceae; Ch, Chenopodiaceae; Cup, Cupressaceae; DA, *Dicksonia Antarctica*; Dod, *Dodonea* spp.; Fab, Fabaceae; HI, *Histiopteris incise*; Indet, indeterminate pollen grains; Isp, *Isoetes* spp.; Lin, Lindseae LF, *Lagarostrobos franklinii*; Mon, monolete psilate spore; Msp, *Micrantheum* spp.; NC, *Nothofagus cunninghamii*; PA, *Phyllocladus aspleniifolius*; Plantago, *Plantago* spp. (native); PlantagoL, *Plantago lanceolata*; Pom, *Pomaderris apetala*; TL, *Tasmannia lanceolata*.

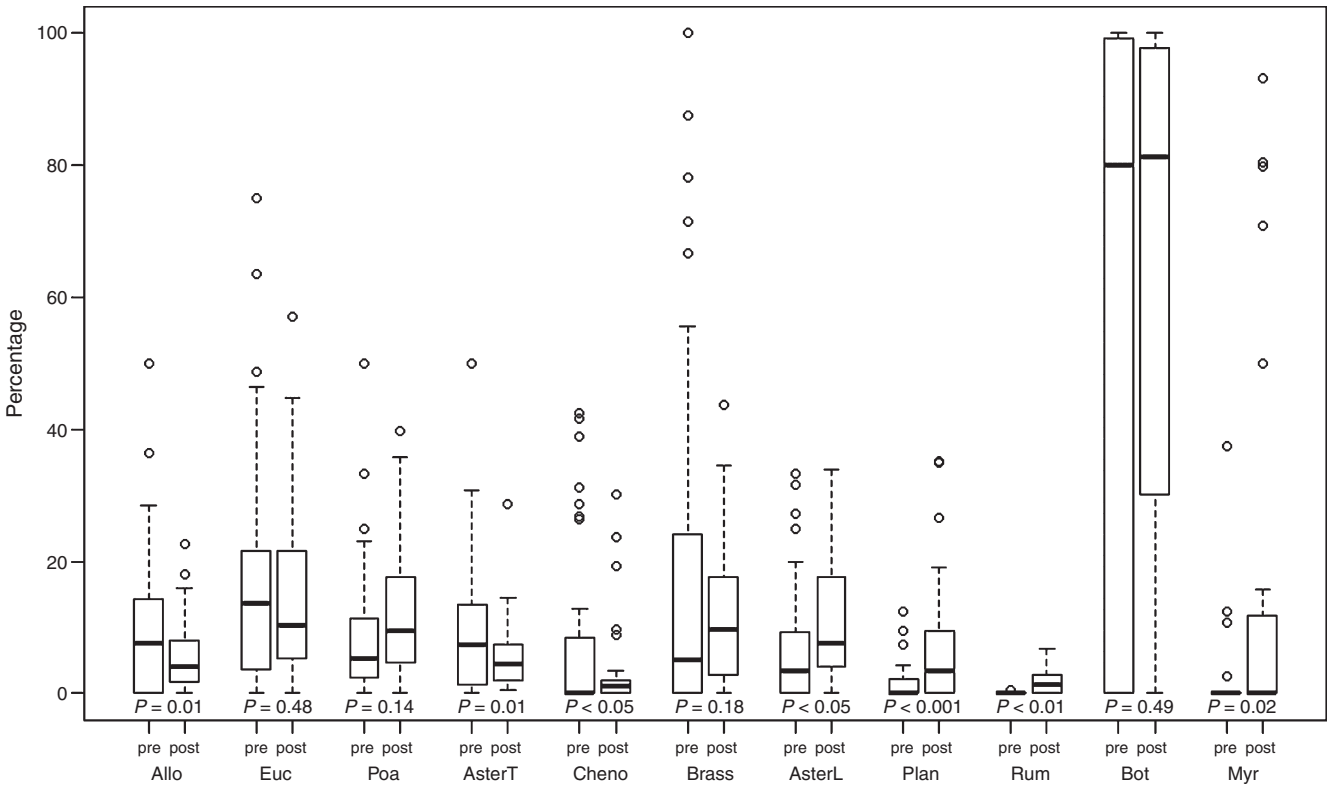

Fig. 4. Differences in the pre- and post-European patterns for pollen data derived from a combined analysis of the 6 sediment cores: showing the dominant dry forest tree taxa, *Allocasuarina* (Allo) and *Eucalyptus* (Euc), native herbaceous taxa, Poaceae (Poa), Asteraceae (Tubuliflorae) (AsterT) and Chenopodiaceae (Cheno), exotic ruderals, Brassicaceae (Brass), Asteraceae (Liguliflorae) (AsterL), *Plantago lanceolata* (Plan) and *Rumex* spp. (Rum) and aquatic taxa, *Botryococcus* spp. (Bot) and *Myriophyllum* spp. (Myr). Pollen values are proportions relative to selected pollen sums (see Fig. 2) and have been converted to percentages for presentation. Probablility values based on generalised linear models are shown for each contrast.

significantly decreasing (Fig. 4). Two of the remaining herbaceous taxa examined probably represent a mix of both exotic and native species; native Asteraceae (Liguliflorae) and Brassicaceae species are rare today but they have a strong representation in the early period. Both of these groups have been replaced by exotic ruderal species as indicated by a significant increase in Asteraceae (Liguliflorae) type pollen and an increase in the median value of Brassicaceae pollen in the post-settlement period (Fig. 4). *Plantago lanceolata* is an exclusively exotic species that appeared earlier in the sediment record than the exotic indicator taxa, *Pinus*, at two wetlands (Fig. 4).

The most abundant aquatic taxon was *Botryococcus* spp., it was present at each of the six wetlands examined and made up ~80% of the aquatic record with no significant change in abundance found between the pre- and post-European periods ($P = 0.49$). There was a significant increase in *Myriophyllum* spp. ($P = 0.02$) after European settlement (Fig. 4).

Minor taxa

Amongst the 6 wetlands, rainforest components, such as *Nothofagus cunninghamii*, *Pomaderris apetala* type and *Phyllocladus aspleniifolius*, were a minor background element (<9%) of total terrestrial pollen. Dry forest species, such as *Acacia* spp., *Banksia marginata* and undifferentiated Fabaceae species, made up a very low proportion of the total terrestrial pollen, typically individual species comprised less than 6% of the total terrestrial pollen in each core. The highest diversity was found in herbaceous taxa and these were in aggregate more abundant than the previously mentioned groups. *Rumex* was the only taxon to show a statistically significant ($P = 0.003$) increase (mean 0.01% to 1.7%) from the pre- to post-European period (Fig. 4). Pteridophyte taxa had constant low background levels ($\leq$3%) in all the cores. *Isoetes* was present in all wetlands in both time periods albeit with highly variable levels.

There were only seven aquatic or wetland species represented in the pollen records. None of the minor aquatic species changed in abundance between the two periods. Restionaceae was the only minor wetland family found at all wetlands, it made up 0.3–6% of the aquatic pollen assemblage.

Charcoal

The amount of charcoal preserved at the individual wetlands varied considerably. The amount of macro charcoal preserved in all six sampled wetlands increased from the pre-European (median = 1.6 pieces cm^{-3}) to the post settlement periods (median = 6.8 pieces cm^{-3}) ($U = 3215$, $P < 0.001$) (Fig. 5).

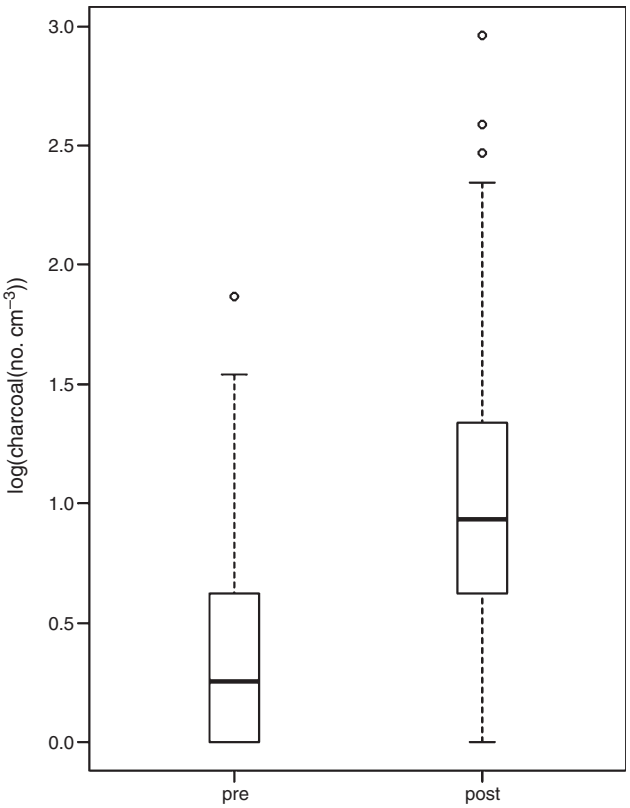

Fig. 5. Boxplots of the differences in the pre- and post-European periods for the macro-charcoal record of six wetlands' sediment cores. Charcoal concentrations of the two periods are log-transformed and differ at the 0.001 level according to a Mann–Whitney test. The pre-European abundance is shown on the left, post-European on the right.

Discussion

Until now there have been few attempts to examine the interplay of vegetation and fire in the dry eastern side of Tasmania, particularly the Midlands (Fensham 1989; Jones 2008; von Platen *et al*. 2011). Most of the historical research in southern Australia has relied upon the accounts of early settlers to evaluate the fire regime of Aboriginal peoples. The paucity of palaeoecological research in this region has been, in part, due to poor pollen preservation and the difficulties in examining sediment records from seasonally dry lagoons because pollen preservation can be inadequate (Thomas 1991) and ^{210}Pb dating can become problematic because drying of sediments may facilitate the downcore movement of ^{210}Pb, which can lead to an underestimate of age at any given depth (Higuera *et al*. 2005). Our approach of using a network of cores enabled us to select a site with good pollen preservation that was suitable for building a chronology, and use other less sensitive sites to draw landscape-level inferences based on statistical analysis of pollen and charcoal in samples amalgamated using a *Pinus* pollen as a marker of European settlement.

Our study demonstrates marked ecological changes in the Tasmanian Midlands following the establishment of a neo-European agricultural landscape. These include a change in woody and herbaceous species abundance associated with native vegetation clearing and the introduction of exotic pasture species. In addition we found a dramatic increase in fire activity in the terrestrial environment and changed hydrological conditions in wetlands. These findings concur with our research expectations and the findings of previous research (Kershaw *et al*. 1994). In contrast to previous research, however, we found no change in sedimentation rate (Dodson and Mooney 2002). We avoided problems with dating by using *Pinus* as a proxy for the post-settlement period, exotic indicator species have been used to demarcate the arrival of Europeans in both Australia (Kershaw *et al*. 1994; Grayson *et al*. 1998; Kenyon and Rutherfurd 1999) and America (van Zant *et al*. 1979).

Palaeoecological studies in southern Australia using pollen and charcoal to reconstruct pre-European fire regimes are beginning to reveal the dynamic nature of fire frequency and impact on vegetation during the Holocene although the interpretation of these data is not clear cut (Mooney *et al*. 2001; Fletcher *et al*. 2014). Charcoal peaks in sediments are more likely to reflect high intensity fires (Whitlock and Larsen 2001; Higuera *et al*. 2010). However, the absence of charcoal in a sedimentary record does not necessary equate to an absence of fire. Low intensity fires produce high levels of incompletely burned particulate matter but this effect is counteracted because these fires are typically small in extent, leaving a small signature in the pollen record (Whitlock and Larsen 2001; Higuera *et al*. 2010). Indeed, Mooney *et al*. (2011) argued that the presence or absence of sedimentary charcoal may be a poor indicator of low intensity fires thought to characterise Aboriginal burning patterns. Studies of traditional Aboriginal fire usage in northern Australia have demonstrated a regime of frequent and patchy fire (Bowman *et al*. 2001, 2004; Bliege Bird *et al*. 2008; Trauernicht *et al*. 2015). They used fire to maintain open grassy landscapes to increase the abundance of game species (Murphy and Bowman 2007; Codding *et al*. 2014) and motivations are assumed to be similar in southern Australia. Dendrochronological evidence shows that dry forests to the east of the study region persisted through increased burning after Europeans arrival, from ~0.7 fires per decade under Aboriginal management to 1.7 per decade in the post settlement period (von Platen *et al*. 2011).

Previous studies on mainland south-east Australia have found an increase in charcoal after European settlement (Johnson 2000; Mooney and Dodson 2001; Mooney *et al*. 2001, 2011). Likewise, the charcoal from Diprose Lagoon record showed that there was a sharp increase in charcoal production concurrent with the appearance of *Pinus* in the sediment record. We suggest the source of this charcoal is the combined effects of using fire to clear land and setting geographically large grass fires to stimulate pasture production (Kirkpatrick 2007). In the Diprose core charcoal production in the 1950s declined possibly reflecting a dwindling of tree-clearing and associated burning, and greater use of mechanised agriculture.

The greater abundance of *Allocasuarina* in the period before European settlement suggests that fire regimes were favourable for this species and other relatively fire sensitive species, and that clearing, grazing and an increase in burning by Europeans caused *Allocasuarina* to decline. This inference is supported

by the post-fire regeneration strategies of the two *Allocasuarina* species found in the Midlands. *A. littoralis* is a serotinous obligate seeder that has low fire resistance (Morrison and Renwick 2000; Burley *et al*. 2007), while *A. verticillata* is also serotinous but has a limited capacity to resprout from rootstock (Singh and Geissler 1985; Ladd 1988). Both species regenerate prolifically after fire as they release a heavy rain of seed onto disturbed ground (Ladd 1988) but require at least 5–6 years fire free to begin producing its serotinous seed (Hueneke 1976; Singh and Geissler 1985). A similar pattern of early and rapid decline of *Allocasuarina* has been found in other temperate savannas of southern Australia (Kershaw *et al*. 1994; Mooney and Dodson 2001; Bickford *et al*. 2008; Jones 2008).

We found no significant change in the abundance of *Eucalyptus* pollen following European settlement. This lack of change in *Eucalyptus* was unexpected given the well documented loss of tree cover in the Midlands, which has occurred since European settlement (Fensham and Kirkpatrick 1989; Prior *et al*. 2013; Romanin *et al*. 2015) and may be an artefact of the amalgamation of data from multiple cores. In highly disturbed agricultural areas of New South Wales a similar lack of change in the pollen signature of *Eucalyptus* has been identified with the suggestion that clearing of woodland trees has been compensated by the planting of other species of eucalypts around homesteads or as windbreaks (Kershaw *et al*. 1994). A lack of overall change may also be evidence of thickening of native remnant vegetation after Aboriginal fire management was disrupted (Gammage 2008). Or alternatively, as tree density decreased, flowering, and therefore pollen production, may have increased and left the pollen signature unchanged (Williams *et al*. 2006); the relevance of this to woodland eucalypt species is , however, largely unknown.

These sediment cores provide further circumstantial evidence for a change in the species composition of understorey plants following settlement, including a sharp reduction in abundance of the Aboriginal staple food of southern Australia, *Microseris lanceolata*, or yam daisy (Gott and Murray 1982; Gott 1983, 2005; Clarke 1986). Asteraceae (Liguliflorae) type pollen cannot be identified to species, but except for *M. lanceolata*, *Sonchus megalocarpus* and *Picris angustifolia*, all members in Tasmania are exotic species. *S. megolocarpus* and *P. angustifolia* are only found in coastal regions (http://www.utas.edu.au/dicotkey/dicotkey/AST/gAsteraceae.htm, accessed 17 February 2016), so we attribute this pollen type in the pre-European period to *M. lanceolata. M. lanceolata* numbers would have declined when active Aboriginal management ceased and introduced sheep began eating them (Gott and Murray 1982). Gott and Murray (1982) point out that the invading European species from the Asteraceae (Liguliflorae) group, such as *Hypocharis* and *Leontodon*, are adapted to living with sheep and cattle and would have outcompeted *M. lanceolata*.

We found an initial decline then increased abundance of Poaceae in the Midlands following European colonisation. The abundance of Poaceae, in association with *Eucalyptus* and Asteraceae pollen before Europeans arriving supports the notion that eucalypt savanna was the dominant vegetation at the time of colonisation (Ellis and Thomas 1988; Fensham 1989; Kershaw *et al*. 1994). The dramatic loss of native grasslands in the Midlands that has occurred in the 20th century (Gilfedder 1990) cannot be seen in these sediment records, because native grass species have been replaced by exotic pastures with higher pollen production (Smart *et al*. 1979), especially in the post Second World War period when pasture production was sharply increased (Kirkpatrick 2007). Potentially, quantification of this change from native to exotic grasses could be approximated in future work by measuring the size of Poaceae grains in the sediment record; larger grains may be produced by introduced grass taxa (Kenyon and Rutherfurd 1999; Bickford *et al*. 2008).

Changes in the composition of aquatic taxa were most apparent at Diprose Lagoon, where a shift in composition from *Botryococcus* spp. to *Myriophyllum* spp. in the mid-20th century was detected. *Botryococcus* is an algal genus which requires standing water (Harle *et al*. 1993) whereas *Myriophyllum* spp. is associated with slow flowing water or the margins of streams. We interpret this transition as reflecting the practise of drainage of wetlands to increase agricultural land, thus producing suitable habitat for *Myriophyllum* to establish in impounded and occasionally flowing artificial drainage channels. Across the Midlands, 34% of wetland area has been drained and a further 23% has been affected by artificial changes in water level (Fensham and Kirkpatrick 1989). In addition to changes in water levels, *Botryococcus* is vulnerable to eutrophication, which may have occurred with increased application of artificial fertilisers and associated increased sheep density in the second half of the 20th century (Kellaway 1989; Kirkpatrick 2007). A shift towards *Myriophyllum* and an overall increase in its abundance throughout the region, is somewhat surprising given its sensitivity to salinity and documented salinity increases in the Midlands (Kirkpatrick and Harwood 1983; Bastick and Walker 2000; Bastick and Lynch 2003). However, some species such as *M. salsugineum*, are known to be tolerant of shallow saline waters (Thomas 1991).

We found no change in sedimentation rate at Diprose Lagoon. This was unexpected because most sediment cores from southern Australia show that a clear increase in sedimentation occurred shortly after the arrival of Europeans in the region (Dodson *et al*. 1994*a*, 1994*b*; Mooney and Dodson 2001). Sediment deposition is increased when vegetation cover is removed through fire or tree removal, which allows erosion to occur. An apparent lack of increased sedimentation at Diprose Lagoon could be associated with increased compaction of upper sediments after sheep were introduced and the impact of artificial drainage on catchment hydrology and sedimentation.

Broadly, we support the notion that Aboriginal land management maintained eucalypt savanna and that European disruption of Aboriginal management resulted in changed fire regimes and associated ecological changes, most notably, an increase in fire, a reduction in *Allocasuarina* and increases in exotic taxa. However, we cannot resolve the question of the hypothesised switch from a finer grained to coarse grained spatial pattern of landscape burning that caused the loss of grassland–forest mosaics that lies at the heart of many environmental histories (e.g. Rolls 1981; Jurskis 2000; Gammage 2011). It is possible that integrated studies combining dendrochronology, palynology and charcoal sediment analysis and historical records in the montane grassland-forest mosaics in Tasmania, that are rich in sediment traps and have tree species with annual growth rings, could further

advance this question of the spatio-temporal changes to fire regimes following European disruption of Aboriginal fire management (McWethy *et al*. 2013; Bowman *et al*. 2013; Holz *et al*. 2015).

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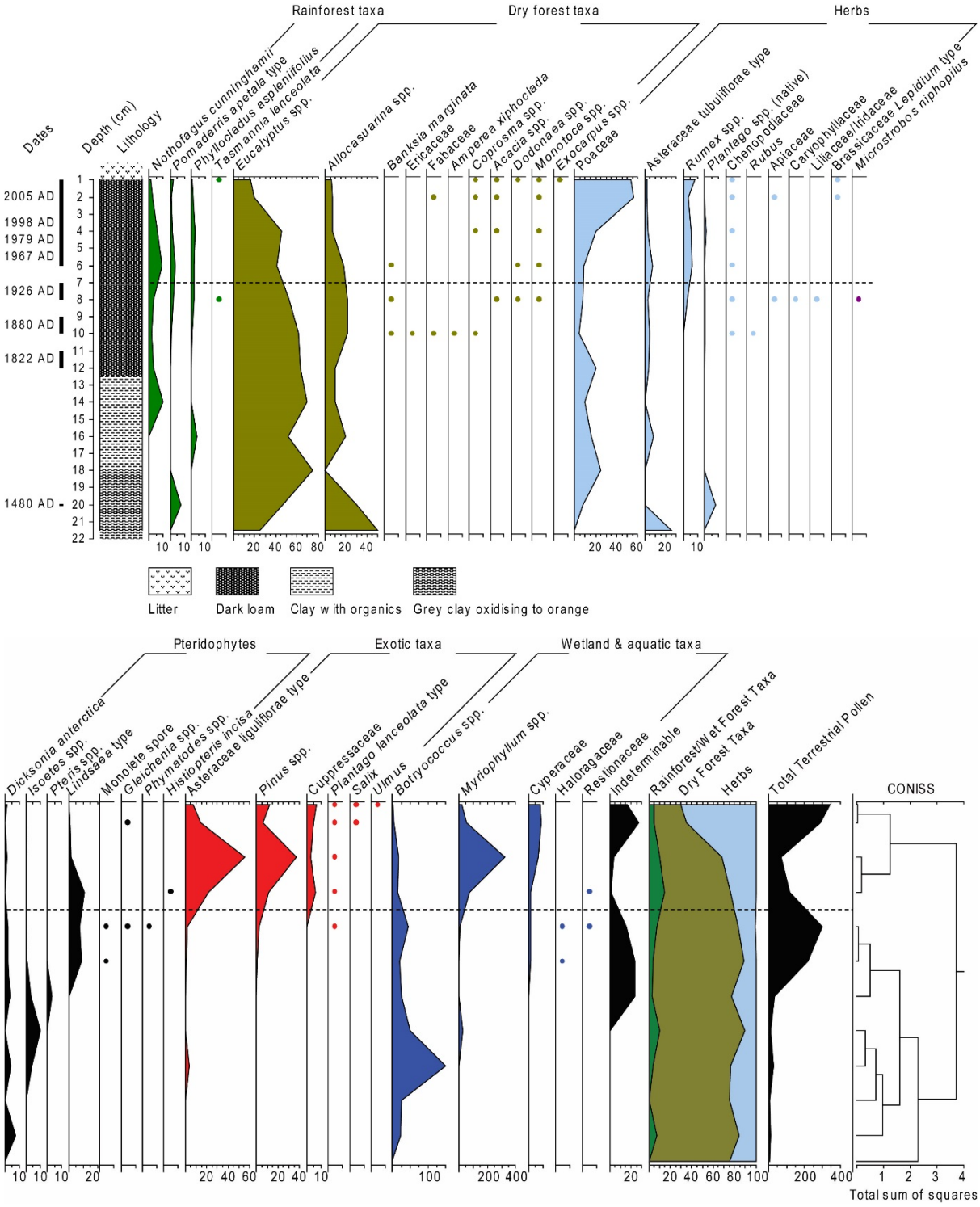
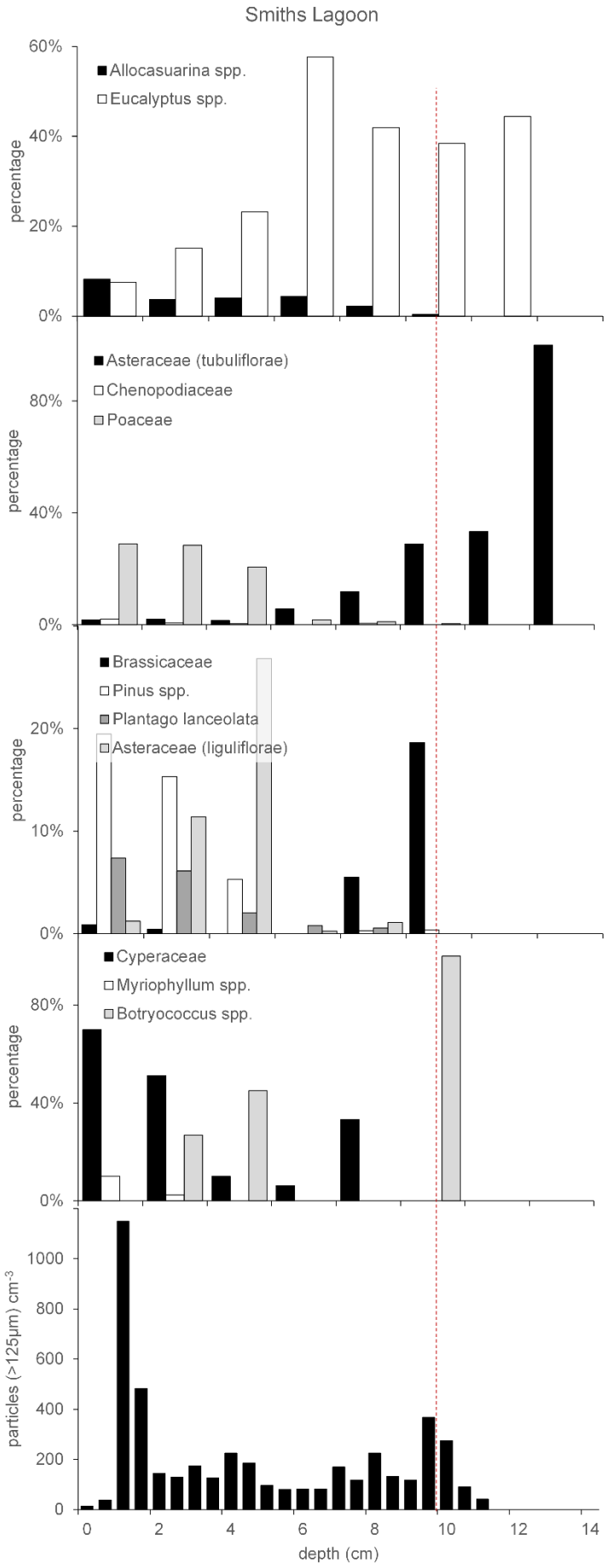
Supplementary materials

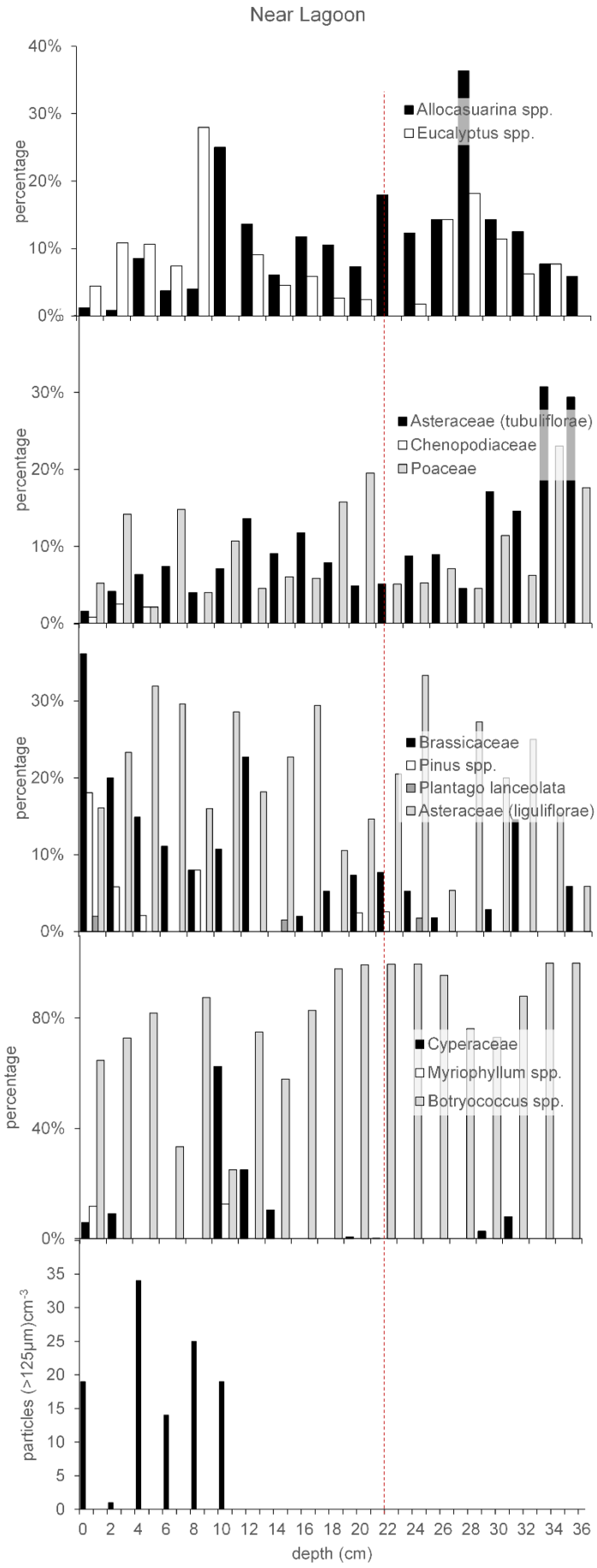
Appendix 1 – Pollen diagram of Diprose Lagoon

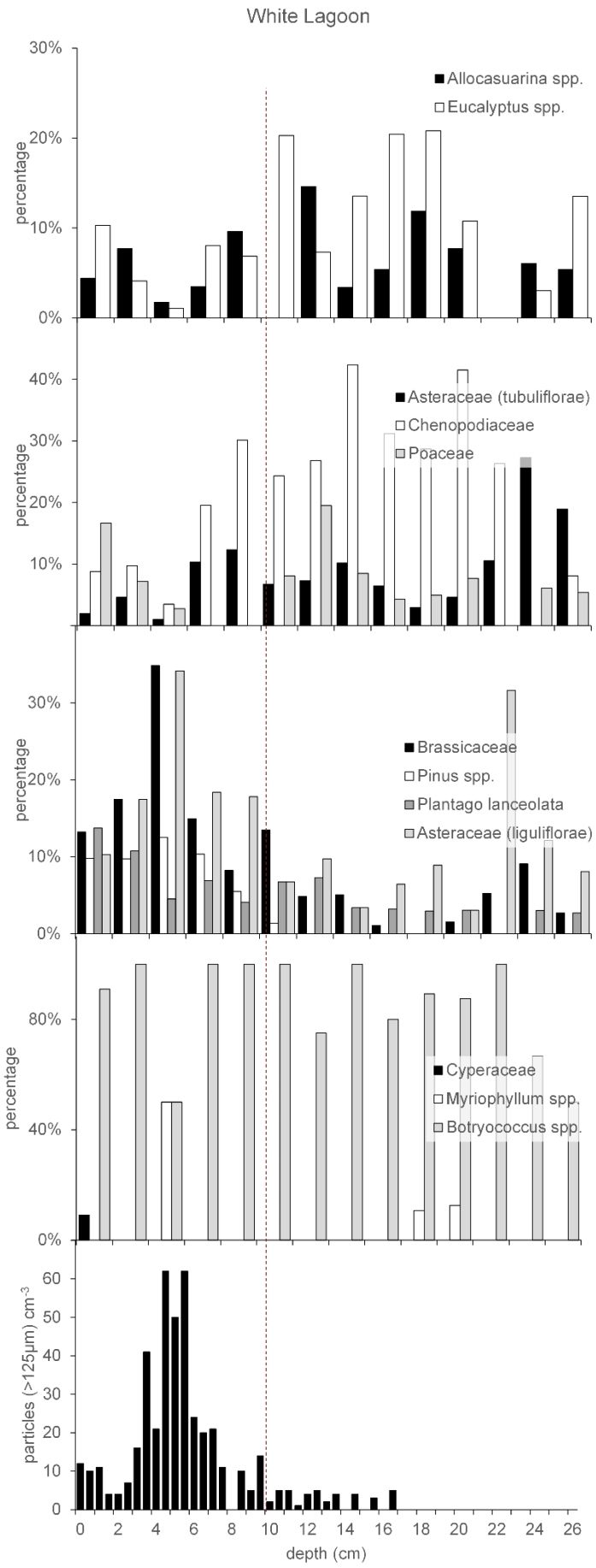


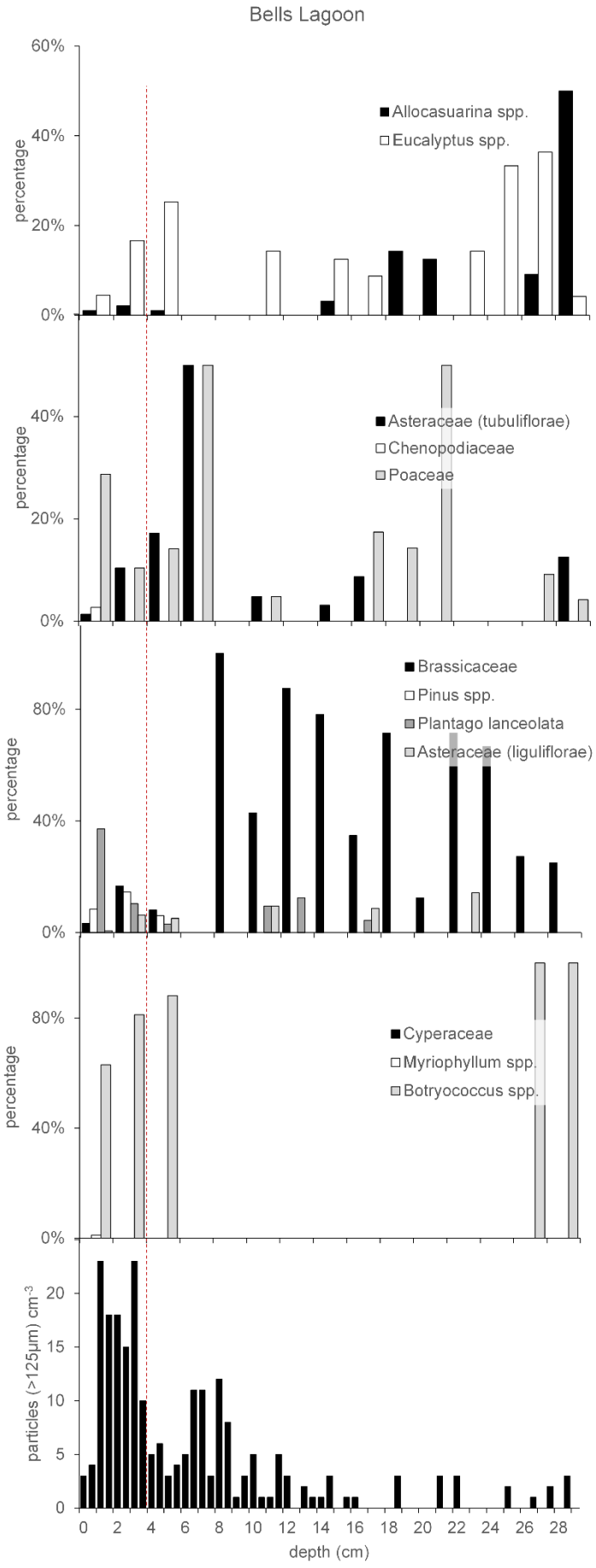
Appendix 2

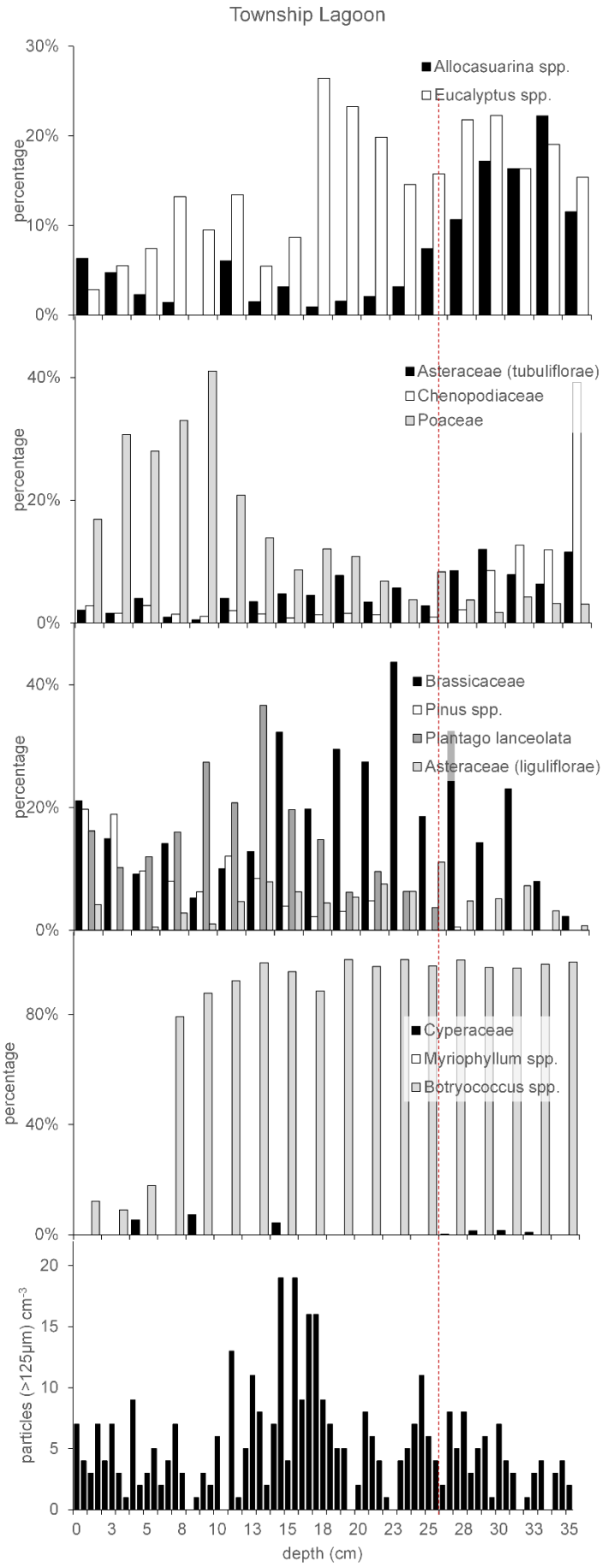
Summaries of the sediment records from six lagoons not discussed in depth in the paper. In each figure, the panels from top to bottom are: dominant tree taxa, *Allocasuarina* spp. and *Eucalyptus* spp.; native herbaceous taxa, Asteraceae (Tubuliflorae), Chenopodiaceae and Poaceae; exotic taxa, Brassicaceae, *Pinus* spp., *Plantago lanceolata* and Asteraceae (Liguliflorae); and aquatic taxa, Cyperaceae, *Myriophyllum* spp. and *Botryococcus* spp. The bottom panel in each figure is the macro-charcoal record. The red dashed line indicates the first appearance of *Pinus* spp. in the record. *Pinus* spp. was found throughout the entire Cleveland Lagoon record so no red line is included.

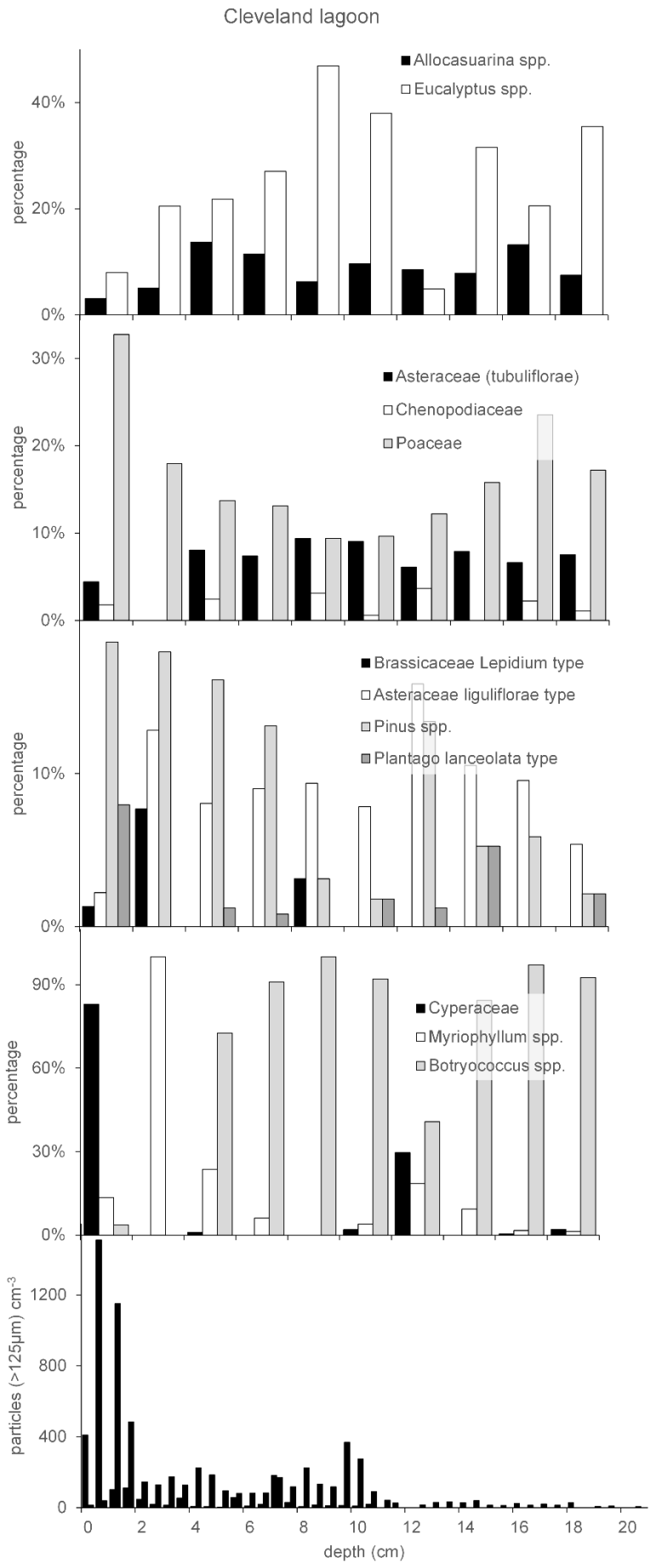

Smiths Lagoon
Allocasuarina spp.
Eucalyptus spp.
percentage
60%
40%
20%
0%
Asteraceae (tubuliflorae)
Chenopodiaceae
Poaceae
80%
40%
0%
Brassicaceae
Pinus spp.
Plantago lanceolata
Asteraceae (liguliflorae)
20%
10%
0%
Cyperaceae
Myriophyllum spp.
Botryococcus spp.
80%
40%
0%
particles (>125µm) cm-3
1000
800
600
400
200
0
0
2
4
6
8
10
12
14
depth (cm)


Near Lagoon
percentage
Allocasuarina spp.
Eucalyptus spp.
Asteraceae (tubuliflorae)
Chenopodiaceae
Poaceae
Brassicaceae
Pinus spp.
Plantago lanceolata
Asteraceae (liguliflorae)
Cyperaceae
Myriophyllum spp.
Botryococcus spp.
particles (>125µm)cm-3
depth (cm)


White Lagoon
30%
20%
10%
0%
percentage
Allocasuarina spp.
Eucalyptus spp.
40%
30%
20%
10%
percentage
Asteraceae (tubuliflorae)
Chenopodiaceae
Poaceae
30%
20%
10%
0%
percentage
Brassicaceae
Pinus spp.
Plantago lanceolata
Asteraceae (liguliflorae)
80%
40%
0%
percentage
Cyperaceae
Myriophyllum spp.
Botryococcus spp.
60
50
40
30
20
10
0
particles (>125µm) cm-3
0 2 4 6 8 10 12 14 16 18 20 22 24 26
depth (cm)


Bells Lagoon
60%
40%
20%
0%
percentage
Allocasuarina spp.
Eucalyptus spp.
40%
20%
0%
percentage
Asteraceae (tubuliflorae)
Chenopodiaceae
Poaceae
80%
40%
0%
percentage
Brassicaceae
Pinus spp.
Plantago lanceolata
Asteraceae (liguliflorae)
80%
40%
0%
percentage
Cyperaceae
Myriophyllum spp.
Botryococcus spp.
20
15
10
5
0
particles (>125µm) cm-3
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28
depth (cm)


Township Lagoon
30%
20%
10%
0%
percentage
Allocasuarina spp.
Eucalyptus spp.
40%
20%
0%
percentage
Asteraceae (tubuliflorae)
Chenopodiaceae
Poaceae
40%
20%
0%
percentage
Brassicaceae
Pinus spp.
Plantago lanceolata
Asteraceae (liguliflorae)
80%
40%
0%
percentage
Cyperaceae
Myriophyllum spp.
Botryococcus spp.
20
15
10
5
0
particles (>125µm) cm-3
0 3 5 8 10 13 15 18 20 23 25 28 30 33 35
depth (cm)


Cleveland lagoon
Allocasuarina spp.
Eucalyptus spp.
percentage
40%
20%
0%
Asteraceae (tubuliflorae)
Chenopodiaceae
Poaceae
30%
20%
10%
0%
Brassicaceae Lepidium type
Asteraceae liguliflorae type
Pinus spp.
Plantago lanceolata type
10%
0%
Cyperaceae
Myriophyllum spp.
Botryococcus spp.
90%
60%
30%
0%
particles (>125µm) cm-3
1200
800
400
0
0
2
4
6
8
10
12
14
16
18
20
depth (cm)

Chapter 2

Trajectory of change in land cover and carbon stocks following European settlement in Tasmania, Australia

Louise M Romanin, Lynda D Prior, Grant J Williamson, David M J S Bowman

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'I know why there are so many people who love chopping wood. In this activity one immediately sees the results.'

– Albert Einstein

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Trajectory of change in land cover and carbon stocks following European settlement in Tasmania, Australia

Louise M. Romanin*, Lynda D. Prior, Grant J. Williamson, David M.J.S. Bowman

School of Biological Science, University of Tasmania, Private Bag 55, Hobart, Tasmania 7001, Australia

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ABSTRACT

The conversion of temperate biomes in the Americas, Australia and New Zealand by European colonists, creating 'neo-European landscapes', is emblematic of the global environmental change inherent in the Anthropocene concept. The Midlands of Tasmania is a valuable model system for studying changes to land cover and above ground biomass in neo-European landscapes. Europeans colonized this area in early 19th century and disrupted a hunter-gatherer economy that has persisted for over 30,000 years. Aerial imagery, historical reconstructions, field surveys and future climate projections provided tools to chart changes in tree canopy cover and carbon stores in the Northern Midlands for the period 1788–2070. In the ~160 years between 1788 and 1940s, large areas of open woodland were cleared but carbon loss was modest (−14 %). In the ~60 years between 1940s and 2010, carbon loss accelerated (a further −21%) as clearing shifted from woodlands to forests. An estimated ~28% of the study area would need to be replanted with eucalypt plantations to capture the carbon lost between 1788 and 2010. Three general circulation models (GCMs) representing climate predictions for 2070 suggest that carbon storage in the landscape would change by +13% to −13.2% of 2010 levels, without any restoration intervention.

1. Introduction

Clearing native vegetation at a broad scale is a potent driver of global loss of biodiversity (Vitousek, 1997; Sanderson et al., 2002; Monastersky, 2014) and a major anthropogenic source of atmospheric CO_2 (Le Quéré et al., 2009). Creating arable land is a prime motivation for clearing vegetation. This process has occurred since the development of agriculture in the mid to late Holocene. In the 18th–19th centuries, European colonisation created agricultural landscapes in North America, Australia, New Zealand and southern South America (Crosby, 1986). These 'neo-European' agricultural areas were typically previously modified by indigenous people, especially through the use of fire to clear and alter vegetation structure and composition (Jones, 1969; Weiser and Lepofsky, 2009; Lightfoot et al., 2013).

Neo-European landscapes present interesting case studies of the interplay of culture and environmental change that is at the root of the Anthropocene concept. We use the term 'Anthropocene' as a metaphor to frame human impacts on the Earth system in both the prehistoric and historic period rather than specifying a precise time frame. Such temporal ambiguity is justified because of the long history of human impacts on the Earth System, beginning with the hunting of megafauna and burning of landscapes by humans and our antecedents in the Pleistocene (Glikson, 2013; Foley et al., 2013; Bowman, 2014). The development of agriculture in the Holocene increased human impacts on the Earth System (Ruddiman, 2003; Ruddiman, 2005; Ruddiman, 2007). Undoubtedly, the Industrial Revolution, often used to demarcate the start of the Anthropocene, has triggered ongoing planetary-wide impacts associated with burning fossil biomass, rapid growth in human populations and land cover change. Since the Second World War (WWII) a step change occurred in impacts on the Earth system, a period Steffen et al. (2007) termed 'the great acceleration' due to rising resource consumption, human population growth and powerful technologies resulting in more intensive and widespread negative impacts on natural landscapes (Crutzen and Steffen, 2003; Ellis et al., 2010).

The Midlands of Tasmania provides an excellent case study to document the rapid transition from hunter-gatherer to modern temperate agricultural landscapes that is at the core the Anthropocene concept. The Midlands is the second oldest agricultural landscape in Australia, settled in the first decade of the 19th century (Fensham, 1989). Before European colonisation in 1802, Tasmanian Aboriginal hunter and gatherers existed on the island for over 35,000 years (Colhoun and Shimeld, 2012). Palaeoecological evidence points to ecological disruptions caused

* Corresponding author.
E-mail address: louise.romanin@utas.edu.au (L.M. Romanin).

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2213-3054/

by Aboriginal colonisation in the late Pleistocene, including changed fire regimes and loss of marsupial megafauna (Turney et al., 2008). Despite these disruptions, the available evidence suggests that, throughout the Holocene, Aborigines had achieved ecological sustainability, coexisting with a rich biota, including numerous endemic plant and animal species that have become extinct or threatened with extinction following European colonisation (Bowman, 1998; Fletcher and Thomas, 2007; Fletcher and Thomas, 2010). Like other Australian Aboriginal cultures, a key aspect of the Tasmanian's economy was the use of fire (Jones, 1969). Aboriginal landscape burning is thought to have maintained the grasslands and open grassy woodlands, which were rich in game (Gammage, 2008; Bowman et al., 2013). Such open vegetation proved ideal for European sheep grazing. By 1825 (Fensham, 1989; Morgan, 1992), most of the grassy lowlands of the Midlands had been allocated to free settlers, and the Aborigines were expatriated (Ryan, 2012).

Over the last 200 years, pastoralists cleared the Midlands to increase grass cover. This clearing targeted the most productive vegetation types, with a particularly intense period of tree removal following WWII, when artificial fertilisers, heavier machinery and the introduction of exotic grasses vastly improved the productivity of grazing lands (Kirkpatrick, 2007; Prior et al., 2013). In the past 20 years, large areas of Tasmania have been planted with fast growing eucalypts for woodchips. This region is too dry, however, for commercial forestry (Laffan, 2000). The contemporary landscape has less than 16% of the original native vegetation, which persists in highly fragmented, small and degraded patches (Fensham, 1989). Despite the small areas of remaining trees, land conversion has not ceased, with extensive irrigation programs under way. On the other hand, restoration schemes are designed to increase tree cover in this landscape (Bailey, 2013; Bryan, 2014; Greening Australia 2014a,b).

Using remotely sensed estimates of woody vegetation cover and above ground carbon stocks as response variables, we evaluate land cover changes since establishment of the agricultural landscape in the Midlands. We focus on four periods: (a) 1788, which provides a baseline under hunter-gatherer management, (b) 1800–1945 when agriculture was established, (c) 1945–2010, the period in which the current landscape was created, and (d) plausible future landscapes in 2070. We hypothesized that the first stage (1788–1945) of land cover conversion would have a minor effect on woody tree cover and carbon stocks compared to the second stage (1945–2010). This is because the hunter-gatherers had essentially opened up the landscape for pastoralism through targeted burning, whereas post World War II industrialised agriculture required far more extensive land conversion. By combining plans for intensive agriculture with three climate change scenarios we provide a reference point for current restoration schemes (Bailey, 2013). We estimate the amount of land that would need to be allocated for biosequestration to capture the carbon (a) lost between the 1940s and 2010 and (b) restore pre-agricultural (1788) levels.

2. Methods

2.1. Study region

We focus on land cover change in an area of 645 km^2 in the south of the Northern Midlands bioregion. This area is a broad floor of a north-south oriented graben (Fig. 1) (Fensham, 1989). The climate is classified as temperate with warm summer according to Köppen–Geiger classification (Peel et al., 2007). The region is located in a pronounced rain shadow, which is driest in Tasmania. The annual precipitation of ~500 mm is evenly distributed throughout the year. The area has warm summers and cool

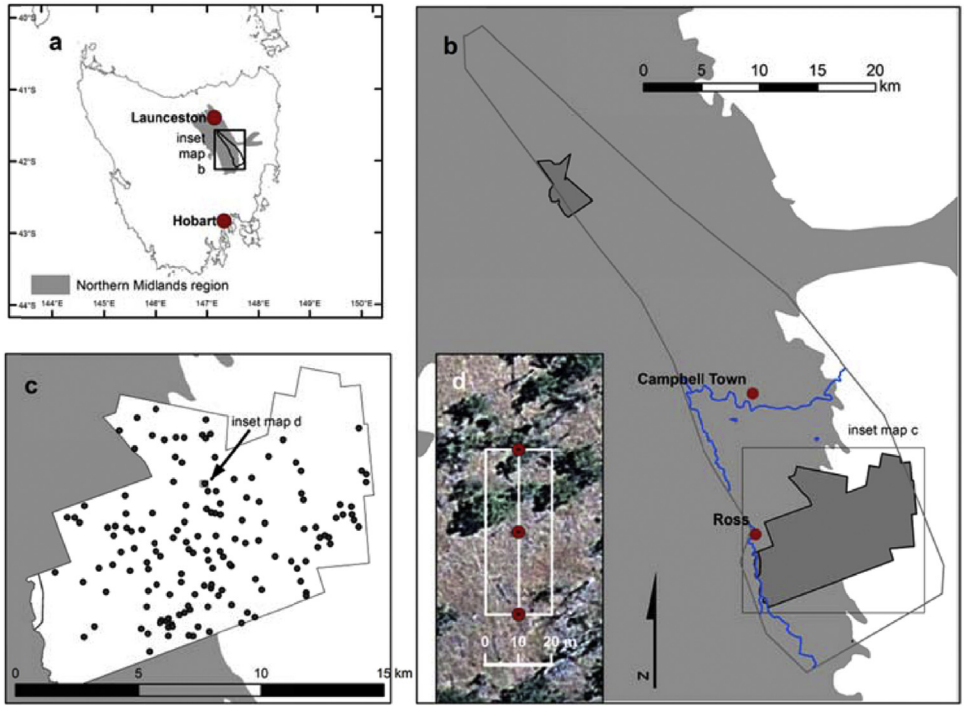

Fig. 1. (a) Map of Tasmania, showing the northern Midlands bioregion (shaded in grey), the cities of Launceston and Hobart and the study region. (b) Map of the study region (outlined), showing the two major towns major rivers in the region (blue) and the two field sites (dark grey), Tom Gibson Reserve in the north and a private property in the south. (c) Location within the private property of the field transects which were used in conjunction with aerial photography to estimate biomass across the study region. (d) Diagram of the field transect drawn to scale and superimposed on a satellite image. The white rectangle represents the belt transect inside which the diameters of all trees were measured. The three red circles indicate points at which tree cover was assessed using a densiometer.

winters; mean daily maximum temperature of hottest month (February) is 24.5 °C and minimum temperature of the coldest month (August) is 1.4 °C. Frost may occur during any month of the year and the average number of frost days across the study area is between 100 and 150 per year (Bureau of Meteorology, 2008). The original vegetation of the area was a mosaic of lowland grasslands and grassy eucalypt woodland (savanna) (Fensham, 1989).

Two sources of remotely sensed imagery were used to examine change in woody vegetation cover over the study region since 1945: aerial photography from the late 1940s (multiple years, black and white), and GeoEye-1 satellite imagery from 2010 to 2012. The aerial photos varied in scale: 1:15,840 for 1945 and 1947, 1:23,760 for 1950 and 1953. The GeoEye-1 imagery was 0.5 m resolution. The 1945 and 1947 photography was scanned at 600 DPI and the remaining at 2136 DPI. TASMAP provided the 1940s aerial imagery (www.tasmap.tas.gov.au), which was orthorectified using Landscape Mapper (Myriax Software, Hobart, Australia). Control points were taken from 2010 to 2012 Taswide Spot imagery, which has high ground-truthed accuracy. The 1788 vegetation patterns were adapted from Fensham (1989).

2.2. Remotely sensed image analysis

We assessed broad changes in woody cover using the 1940s and 2010s imagery. We drew polygons around all woody patches and split them into multiple parts as necessary to account for areas of different tree cover. We assigned each polygon a density score, adapted from the Specht (1970) vegetation classification with height of upper stratum ignored. We classified woody patches with 30–70% cover as open forest, 10–30% cover as woodland, and <10% cover classified as open woodland (Table 1). Areas with ≤1 tree per 10^4 m^2, including cropland, were defined as grasslands.

The map of 1788 vegetation was constructed by Fensham (1989) using historical sources and vegetation surveys. We digitised and orthorectified it in ArcGIS and then classified it according into the same four vegetation categories as those used for the remote sensed imagery. The scale of the map was coarser, and the precision of vegetation types lower, than in the remote sensing analysis.

2.3. Field assessment

We made field measurements of tree size and density for estimating biomass for the study area. We collected field data at 162 transects on a private property in the south of the study region and at Tom Gibson Nature Reserve (managed by Parks & Wildlife Service, Tasmania) in the north (Fig. 1). These two areas contain most of the vegetation types found in the study region. They also capture a cross section of different land management and conservation practices. We selected transects randomly from the most recent imagery and allocated them to the four vegetation classes.

At each field site, we established a belt-transect 50 m long and 20 m wide. These transects ran either north–south or east–west, randomly decided upon a toss of a coin. We made densiometer readings at three points along the transect and averaged them to assess canopy cover from the ground. We also measured the diameter at breast height (DBH; 130 cm above the ground) of all trees (≥10 cm DBH), and saplings (>1.5 m tall and <10 cm DBH). We also assessed trees and saplings as alive or dead, and identified to species.

We measured woody debris in each transect using a modified line intersect sampling method (Marshall et al., 2000). We measured the diameter of all fine woody debris (FWD) (>1 cm–<10 cm) and coarse woody debris (CWD) (>10 cm) that crossed the midline of each transect. We calculated the volume per 10^4 m^2 of CWD and FWD for each transect using the formula in which all pieces are assumed to lie almost horizontal:

$$\mathrm{CWD} = \frac{\pi^2}{8L} \times \sum_{i=1}^{n} d_i^2$$

where CWD is the volume of debris (m^3 10^4 m^{-2}), L is transect length (m) and d_i is the diameter of the ith branch or log (cm) (Marshall et al., 2000).

2.4. Biomass calculations

We estimated the above ground biomass at each transect from the DBH measurements of all trees and saplings, using generic allometric equations (Paul et al., 2013). This equation applies to trees up to 100 cm DBH. Above this size, therefore, carbon may be overestimated. Reliable functions for larger trees are not yet available, however, so their development is an active field of research (Keith et al., 2009). Because only 0.9% of trees sampled were over 100 cm DBH, the error in our biomass estimates is small. We then estimated below ground biomass using a factor of 0.25 for live trees and 0.2 for dead trees (Keith et al., 2000). We then converted biomass to carbon using factors of 0.5 for live trees, and 0.45 for dead trees (Gifford, 2000).

We calculated the carbon in CWD and FWD at each transect using the formula:

$$\mathrm{C} = \text{Volume per} 10^4 \mathrm{m}^2 \times \text{Density Factor} \times \text{Density} \times \text{Carbon Factor}$$

We assumed a mean decay factor of 2 and density factor of 0.68 for all CWD. We calculated the mean density of wood before decay from the dominant eucalypts in the study region (*Eucalyptus amygdalina*, *Eucalyptus delegatensis*, *Eucalyptus pauciflora*, *Eucalyptus viminalis*, *Eucalyptus ovata*) as 567.7 kg m^3 (Ilic et al., 2000). The carbon factor was 0.49 (Gifford, 2000).

We determined the carbon density (total mass of carbon per m^2) at each transect by summing above ground biomass, below ground biomass and mass of woody debris. We then calculated average values for each vegetation category (Table 2). These values were multiplied by the ground area of each category for each period in the digital mapping to get a total carbon estimate for 1788, 1940s and 2010s.

2.5. Future tree cover in the Midlands

To estimate the tree cover in the study region into the future, we used Williamson et al.'s (2014) eucalypt cover projections for 2070.

Table 1
The vegetation classification categories of the various sources of data used in the study (Specht, 1970; Fensham, 1989).

Specht classification	Tree density	Fensham classification	Field transects (n)
Grassland	≤1 tree 10^4 m^2	Treeless	38
Open woodland	<10% canopy cover	Open-woodland	28
Woodland	10–30% canopy cover	Woodland	24
Open forest	30–70% canopy cover	Forest	72

Table 2
Average carbon density estimates (kg m^{-2}) and standard error (S.E.) for woody debris, standing dead and live trees by vegetation category. The proportion of each component for each vegetation group is also presented. The mean density of stems per 10^4 m^2 and diameter at breast height (DBH), total and broken down by *Eucalyptus* and *Acacia*, for each vegetation category is included.

	Grassland (<1 tree 10^4 m^2)	Open Woodland (<10% cover)	Woodland (10–30% cover)	Open Forest (30–70% cover)
Total carbon (±S.E.)	1.29 (0.63)	5.0 (1.54)	9.75 (1.61)	17.73 (1.27)
Woody debris	4%	7%	8%	9%
Standing dead	33%	41%	28%	16%
Live trees	63%	53%	64%	75%
Stems 10^4 m^{-2}	10.3	36.4	146.7	730.4
Eucalyptus	59%	62%	28%	36%
Acacia	10%	35%	71%	59%
Mean DBH (±S.E.)				
Eucalyptus	54.0 (6.5)	54.8 (4.3)	40.5 (2.4)	26.2 (0.6)
Acacia	17.3 (2.8)	27.3 (2.8)	11.1 (0.9)	5.5 (0.1)

These projections are based on the relationship derived between eucalypt cover and current mean annual precipitation and annual water balance for southeast Australia. Three dynamically downscaled general circulation models (GCMs), run under a high greenhouse gas emission scenario (the A2 scenario from the IPCC Special Report on Emissions Scenarios (SRES), provided the basis for Williamson et al.'s (2014) climate projections (Nakicenovic and Swart, 2000)). The three GCMs were chosen to represent the most contrasting future predictions; (1) CSIRO-Mk3.5, (2) MIROC3.2 (medres), and (3) UKMO-HadCM3. Based on these three GCMs, Williamson et al. (2014) projected the following changes in tree cover for the northern Midlands: CSIRO-Mk3.5, −13.2%; MIROC3.2 (medres,), −9.8%; and UKMO-HadCM3, +13.0%. We used these values to predict carbon stores in 2070, based on the current values estimated in this study.

2.6. Planting to replace carbon stores

We estimated how much land area would need to be replanted with eucalypts to replace the carbon lost from the landscape since European settlement under the three future GCM scenarios. We created buffers of varying widths along all property boundaries, roads and rivers in currently treeless or lightly treed areas and modelled them as revegetation plantings. We omitted 102.76 km^2 of the study area proposed for an extensive irrigation system. We assumed restoration plantings with a carbon density of 13.2 kg m^{-2} under current climate conditions. This value was based on the average biomass density of mature dry eucalypt forests in Tasmania estimated by Moroni et al. (2010), with 9% added to the original 12.1 kg m^{-2} to account for CWD for forests (Table 2). We scaled the total area of restoration planting for each buffer by changes in the tree cover from Williamson et al. (2014), outlined above.

3. Results

3.1. Biomass and carbon

Comparing of the estimates of remotely sensed tree cover with ground-based densiometer measurements of cover at 164 transects validated our estimate of percentage canopy cover. The mean densiometer values correlated strongly ($r^2 = 0.91$) with, but were lower than, the remotely-sensed values of aerial cover.

A monotonic increase in above ground carbon stocks amongst the four vegetation categories occurred, from around 1.3 kg m^{-2}in grassland to 17.7 kg m^{-2} in open forests (Table 2). Amongst all vegetation types, live trees provide storage for over half of the carbon. Woody debris stored less than 10%. We found marked differences in the importance of standing dead trees in storing carbon. This pool accounted for only 15% of the carbon in the open forest and over one third in the grassland and open woodland, reflecting the impact of the decline in paddock trees. For all vegetation types, the biomass measured was concentrated in eucalypts. These trees occur at lower density but are typically larger than acacias (Table 2).

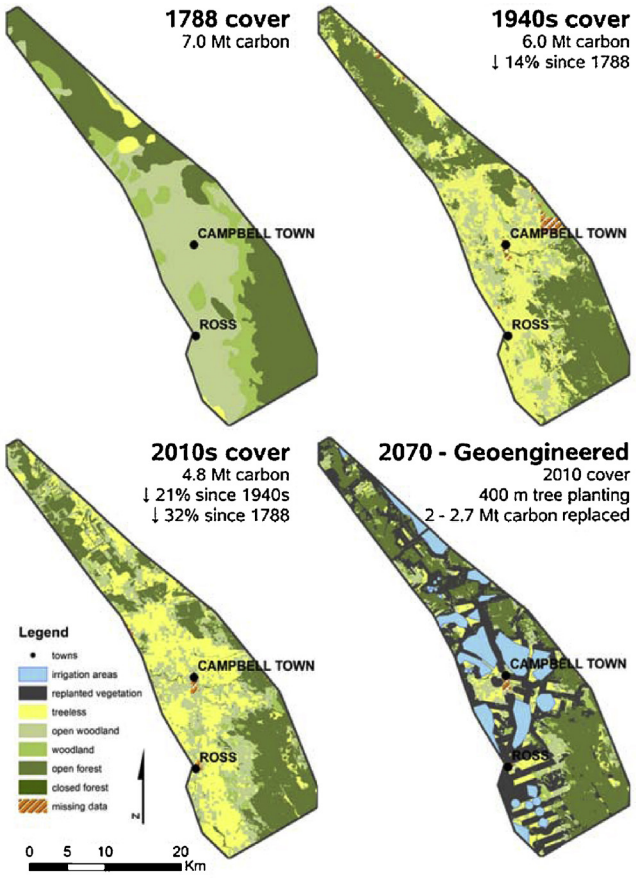

Fig. 2. A time series of woody cover change in the study area from 1788 to 2070. The 1788 map is based on a reconstruction by Fensham (1989), 1940s based on aerial photography and 2010s based on high resolution satellite imagery. The 2070 geoengineered scenario demonstrates the replacement of the 1788–2010s carbon debt and shows 2010s vegetation cover, proposed irrigation areas (blue) and 400 m wide strips of vegetation planted around all roads, property boundaries and rivers at a carbon mass of 13.2 kg m^{-2}.

3.2. Tree cover

From 1788 to 2010s, tree cover declined in the Midlands with a corresponding increase in grassland (Fig. 2). Between 1788 and 1940, one third of the woodlands was lost, as well as approximately one half of the open woodland. The area of open forest remained similar, however (Fig. 3). Between 1940 and 2010, a further decrease in woody cover occurred, with over half the study region converted to grassland. The clearing of open woodland and open forests largely drove this loss.

3.3. Carbon stores

Land clearance resulted in an estimated loss of about one third of the carbon (7–4.8 Mt) from the study area since European arrival (Fig. 4). Most of this loss occurred after WWII. In the ~160 years between 1788 and the late 1940s, approximately 1 Mt (1.56 kg m^{-2}) of carbon was removed from the landscape. In the ~60 years between 1940s and 2010s, about 1.24 Mt of carbon (1.92 kg m^{-2}) was lost from the study area. The clearing of open forests drove these larger losses after WWII, which totalled 19% from the estimated 4.64 Mt of carbon in 1788 (Fig. 3).

3.4. Replacing carbon

To restore the natural vegetation and replace the carbon lost through human activites from 1788s to 2010s, an estimated 178.42 km^2 would need to be planted at a carbon store value of 1.32 kg m^{-2} under current climate conditions (Fig. 5). The area of planting required represents nearly 28% of the entire study region. This area is equivalent to more than 400 m wide eucalypt plantings along every road, property boundary and river (Fig. 2). Under the UKMO-HadCM3 model, carbon storage potential is enhanced compared to both current conditions and the other climate models. Carbon storage in 400 m wide plantings, therefore, could be a total of 0.3 Mt more than if grown under current climate conditions. This storage would be 0.6 Mt more than in the least optimistic climate model, MIROC3.2(medres). The remaining two GCMs would lead to total carbon that was between 0.23 and 0.31 Mt short of replacing the 2.24 Mt carbon debt (Fig. 5). The post-WWII debt is almost replaced with 100 m wide buffers (~10% of study area) under current conditions and UKMO-HadCM3. Under all climate models and current climate, 40 m wide buffers (covering 3.9% of the study region) approximately restore the 1990 carbon debt. These buffers would contribute towards satisfying the requirements of the Kyoto protocol.

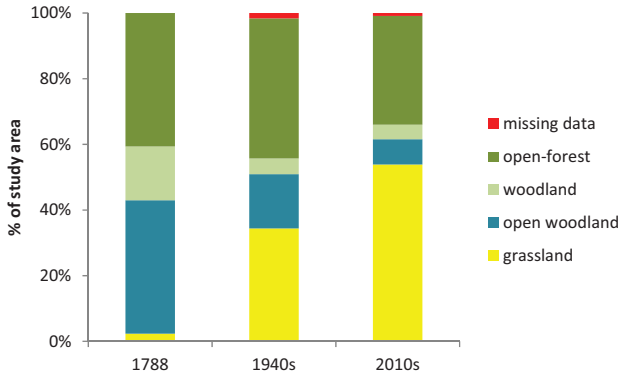

Fig. 3. Changes in the area occupied by different vegetation categories from 1788 to 2010s. Small areas of the remote sensed imagery were not available, resulting in areas of missing data.

If the status quo is maintained and no attempts are made to restore carbon into the landscape, the most optimistic climate model for 2070 used here, UKMO-HadCM3, predicted an increase of 0.62 Mt carbon on current stores (Fig. 4). Little difference was found between the remaining two climate models, which predicted decreases of 0.63 Mt (CSIRO-Mk3.5) and 0.47 Mt (MIROC3.2(medres)) compared with current stores.

4. Discussion

While considerable study has focused on changes in carbon stocks in various woodland vegetation types (Hughes et al., 2006) and changes in extent of temperate savanna (Brewer and Vankat, 2004), few estimates exist of loss of biomass that accompanied the transformation from indigenous management to modern agricultural systems. Houghton et al. (1999) calculated carbon fluxes across North America from 1700 to 1990 arising from changes in land use, including, cropping, wildfire and woody regrowth. To our knowledge, this work is the first attempt to account for carbon loss due to agricultural transformation in Australia.

4.1. Biomass calculations

Our calculated mean carbon density for open forests in the Midlands of 17.7 kg m^{-2} is well within the range of 15.0–25.0 kg m^{-2} reported for dry sclerophyll forests (Grierson et al., 1989; Roxburgh et al., 2006). This estimate is higher than the global value for cool temperate dry forests used by the IPCC, 12.1 kg m^{-2} (Keith et al., 2009). While carbon stores in grassy woodlands are not well documented, the 5.0 kg m^{-2} here in open woodlands are comparable to the range of 3.2–8.7 kg m^{-2} found in New South Wales (Young et al., 2005).

Because no allometric equations exist specifically for the species found in these Tasmanian woodlands and open forests, we used a generic equation (Paul et al., 2013). This equation was developed for trees up to 100 cm DBH, but some of our trees were larger, so we had to extrapolate outside of this range for the larger trees. We therefore potentially overestimated biomass because large trees are often damaged, senescent and contain hollows (Chambers et al., 2001; Roxburgh et al., 2006). A good relationship is unlikely between biomass and diameter for these large veteran trees.

4.2. Historical estimate of changes to land cover and carbon storage

The vegetation reconstruction by Fensham (1989) presents a landscape that was dominated by open woodland or savanna. The savannas allowed the creation of a 'neo-European' landscape by early colonists with relative ease despite clearing being undertaken manually. This rapid clearing of temperate savanna for agriculture is a pattern repeated in large swathes of North America (Conner et al., 2001; Brewer and Vankat, 2004). While we found the carbon loss in the 160-year period between hunter-gatherer management and WWII to be comparatively modest, the decrease in extent of woodlands and open woodlands was dramatic because the early settlers targeted these systems (Fig. 3). We acknowledge the uncertainty in using Fensham's (1989) reconstruction of 1788 vegetation patterns. Even if this reconstruction is near accurate, we could not predict the exact species composition, age- and size-classes and spatial distribution or patchiness of vegetation, which would affect carbon store estimates. For example, large trees contain and sequester more carbon than smaller ones (Stephenson et al., 2014). Many of the trees lost from the landscape were probably large, so we are likely to have underestimated early carbon stores.

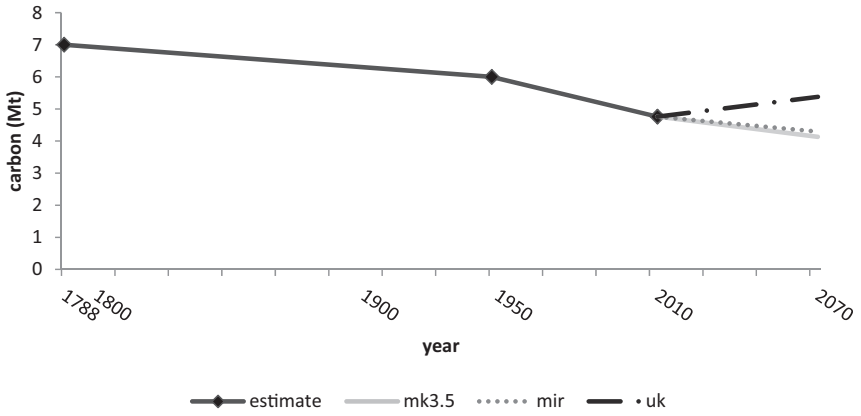

Fig. 4. Changes to total above ground carbon stocks in the study region over time. Less carbon was lost in the 160 years between 1788 and 1940s than during the 60 years between 1940s and 2010s, reflecting the commencement of clearing open forests after WWII. Carbon in the landscape in 2070 was predicted using three climate change scenarios and assuming no attempts were made to restore native vegetation. The most optimistic model was UKMO-HadCM3, which predicted more carbon by 2070 than is currently in the landscape because of greater eucalypt cover. There was little difference between the remaining two models, both predicting stores lower than in the current climate. Climate model abbreviations are UK = UKMO-HadCM3, mk35 = CSIRO-Mk3.5 and mir = MIROC3.2(medres).

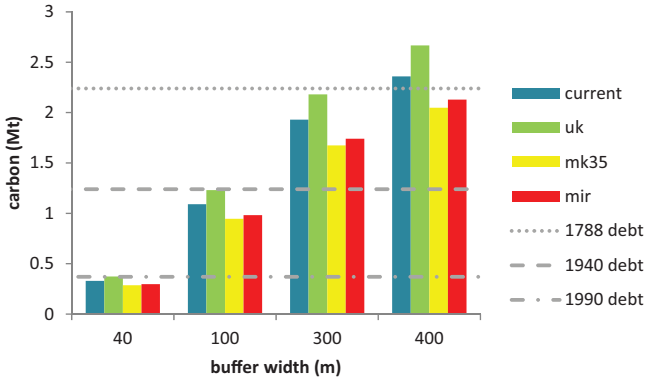

Fig. 5. Revegetation plantings at the carbon density equivalent to a mature dry eucalypt forest (13.2 kg m^{-2}) estimated under different GCMs. More than 100 m buffers around all property boundaries, roads and rivers would be needed to make up the carbon debt accrued from 1940s to 2010s, and approximately 400 m to replace the 1788 debt. The most optimistic model (UKMO-HadCM3) predicts far more carbon in all planting configurations. The debt from 1990 to 2010s would require a little more than 40 m wide plantings to be replaced. The additional loss of carbon that would occur from 2010s to 2070 has not been accounted for here. Climate model abbreviations are UK = UKMO-HadCM3, mir = MIROC3.2(medres) and mk35 = CSIRO-Mk3.5.

The aerial imagery used to examine changes to the landscape between WWII and the present time allowed a greater precision in vegetation mapping and carbon estimates. More carbon was removed from the landscape in the 60 years post-1940s than in the 160 years before (Fig. 4). The greater carbon loss was due to the intensification of agriculture in the region, supporting the notion of 'the great acceleration' in the latter stages of the Anthropocene (Steffen et al., 2007). Although the area of open woodlands continued to decrease appreciably, most of the carbon lost in this period was from open forests, which were targeted as more open, productive areas became scarce (Fensham and Kirkpatrick, 1989). Deliberate removal caused much of the tree loss in the region, especially since the 1970s including 'secondary clearing' such as removal of single trees that stood in the way of increasing larger agricultural machinery and pivot irrigation infrastructure (Prior et al., 2013). The remaining patches of native vegetation are mostly located in areas unsuitable for agriculture, so they are relatively safe from deliberate clearance into the future. However, rural tree decline, a syndrome of premature dieback of trees due to a constellation of stressors including agricultural fertilisers, insect and mammalian herbivores, drought and heat stress, is also a major contributor to tree cover loss (Neyland, 1999; Close and Davidson, 2004; Davidson et al., 2007).

In south eastern Australia and other 'neo-European' regions, biomass has increased in remnant forests and woodlands (Birdsey et al., 1993; Asner et al., 2003; Gibbons et al., 2008; Geddes et al., 2011; Prior et al., 2013). This trend was not evident in our study, but we did detect high density of *Acacia* species with small diameters in the understory of open forests. Although *Acacia* contributed only a small amount (8%) to the estimated biomass of the forests, the abundance of these early-successional plants signals forests recovering from past disturbances (Onans and Parsons, 1980; Grant and Loneragan, 2001; May and Attiwill, 2003). In this area, disturbances were most probably frequent fires set by grazers to increase the abundance of forage for stock and low intensity logging for fencing and firewood.

4.3. Future change to land cover and carbon storage

The main factors likely to affect future tree cover in the Midlands is a new round of intensification of agriculture associated with planned large irrigation schemes, and the effects of climate change on remnant tree populations (Benayas et al., 2008; Plantinga and Wu, 2014). The predictions of future climate change in the Midlands showed considerable variability, primarily because MAP differs under the different climate predictions. The most optimistic model, UKMO-HadCM3, predicted increased rainfall in the Northern Midlands, leading to an increase in the cover of eucalypts. This increase is possible because of enhanced tree growth and survival, and greater recruitment of juveniles. Two of the GCMs predicted hotter and generally drier conditions, and therefore decreased eucalypt cover. This decrease would be a result of both increased mortality and decreased recruitment, which have already been observed in the region (Neyland 1999; Close and Davidson 2004). Thus, although available climate projections show variable trends, tree cover and carbon storage will likely decline due to reduced water balance (Williamson et al., 2014).

Limited water availability and decreasing rainfall since the 1980s have, until now, restricted the extent of cropping in the Midlands (Close and Davidson, 2004). The implementation of an extensive irrigation scheme, however, will encourage a change from grazing to cropping enterprises. Our estimates based on current plans indicate that a 2.4% loss of biomass will occur through clearing for irrigated crops. Additional irrigation water in the landscape could prove detrimental to tree cover through exacerbating dryland salinity (Bastick and Walker, 2000;

Bastick and Lynch, 2003; Davies and Barker, 2005). Given that water balance is crucial in determining eucalypt cover (Williamson et al., 2014), the interactive effects of irrigation and climate change on the persistence or reestablishment of trees in this landscape are worthy of further investigation.

4.4. Replacing the carbon debt with plantations

Establishing restoration plantations has been promoted as a practical way of mitigating increasing CO_2 (Houghton et al., 1999; Bailey, 2013; Plantinga and Wu, 2014). The Midlands plantations are unlikely to repay the current carbon debt incurred because of clearing since European colonisation. To replace the 1788 debt, we suggest that mature plantings at the carbon density of mature open forests would need to cover almost 28% of the study region. These plantings should be located in currently cleared, agricultural land and subject to climate conditions no worse than the current climate. A number of factors make this proposition unreasonable. The density of these plantings is unattainable by 2070. Because of time lags between planting and maturity, temperate sclerophyll forests make take more than 150 years to attain 90% of their carbon carrying capacity and more than 100 years to develop structural complexity (Roxburgh et al., 2006; Vesk et al., 2008). Additionally, densely planted revegetation has less natural recruitment and individuals have slower DBH growth (Vesk et al., 2008). Climate change may increase drought-induced mortality (Allen et al., 2010), increase the risk of destructive fires (Flannigan et al., 2013), and make insect or pathogen outbreaks more frequent (Nelson et al., 2013), thus threatening the persistence of plantations. Although CO_2 fertilisation increases water use efficiency, concurrent increases in tree growth rates have not been observed (Silva et al., 2010; Peñuelas et al., 2011), Therefore, it is unlikely that growth rates will be higher than those observed today. The usual carbon accounting procedure pays a unit price per tonne of CO_2 offset or captured annually (Cacho et al., 2003). Despite this, it is highly unlikely that almost 20% of an agricultural landscape would be surrendered to carbon storage even with financial incentives. It is much more feasible to repay the carbon debt with tree plantings using the 1990 baseline employed by the Kyoto Protocol (Van Kooten, 2000; Cacho et al., 2003). Our calculations suggest that this would entail restoring approximately 4% of the study area with high density plantations. These plantations, while young and with high stem density, would have high carbon sequestration rates per area despite lower per stem accumulation (Xue et al., 2011; Paul et al., 2015). Expecting agricultural regions such as the Tasmanian Midlands to be carbon neutral is unrealistic, so carbon sequestration programs are constrained and best thought of as a subsidiary rather than primary objective. A sensible way to maximise carbon capture for climate change mitigation in Tasmania would be to protect established forests while increasing the forest estate with areas of high-density restoration plantings in underutilised agricultural regions.

Even if restoring carbon to pre-European levels is an unattainable goal, trees must be re-established in this landscape. Biodiverse plantings can remediate damaged agricultural land and restore some of the ecosystem services that have been lost with land-use change (Jackson et al., 2005). Co-benefits of carbon sequestration can include reducing nitrogen runoff, erosion control and salinity control (George et al., 1999; Vesk et al., 2008; Plantinga and Wu, 2014). Salinity is already a risk in the drier parts of the Midlands (Davies and Barker, 2005). A transition to irrigated agriculture is likely to exacerbate this risk (Kokkoris, 2003). Greening Australia's newly established plantings in the region are located on floodplains and along rivers. These areas are sensibly chosen to be beneficial for re-establishing connectivity for wildlife (Bailey, 2013). They are more likely to support faster tree growth than less productive sites (Vesk and Mac Nally, 2006).

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Chapter 3

The legacy of pasture improvement causes recruitment failure in grassy eucalypt woodland conservation reserves in the Midlands of Tasmania

Louise M Romanin, Lynda D Prior, David M J S Bowman

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Abstract Australia's most fragmented and least reserved landscapes are the grassy eucalypt woodlands of the south-east. Two hundred years of agricultural disruption have transformed these landscapes, and agricultural enterprises continue to expand and develop, meaning the threats to these landscapes have not abated. The Tasmanian Midlands is primarily privately owned, with very little area devoted to conservation of biodiversity. In this landscape, conservation covenants have been enacted on many private properties with the intention of encouraging tree recruitment and conservation of threatened plant communities and rare species. Evidence of the effectiveness of these covenants in protecting overstorey tree population health is lacking. This study compared the demographic structures of overstorey *Eucalyptus* species and midstorey tree genera on public and private properties with contrasting land use histories. Reserves on private lands had little tree recruitment, probably because exotic pasture species were common, whereas tree recruitment was abundant in public reserves, where pasture improvement has not occurred. Active measures are needed to restore ecological structure and function in grassy woodland conservation reserves on private land by encouraging regeneration of *Eucalyptus* and *Acacia* species as well as returning the ground layer to a functionally native state. This will entail reinstating fire disturbance, reducing exotic pasture species cover and managing domesticated (sheep), feral (deer) and native (macropod) herbivores.

Additional keywords: recruitment bottleneck, temperate savanna, conservation covenant

Introduction

Some of the most fragmented and least reserved landscapes in Australia are the grassy eucalypt woodlands and grasslands of south east Australia (Kirkpatrick *et al.* 1988; Yates and Hobbs 1997; Lunt *et al.* 2000; McIvor and McIntyre 2002). Early 19th Century European settlers favoured these temperate savanna ecosystems for pastoralism. In a short period, the native vegetation was extensively altered and Aboriginal fire regimes were drastically changed or eliminated. The conversion for agricultural production involved tree clearing, soil cultivation, establishment of high performing exotic pasture species and, in the 20th Century, the application of synthetic fertilizers (Fensham 1989; Lunt 1991; Prober and Thiele 1995). Consequently, small relictual areas of little modified grassy woodland and grassland are now isolated in a matrix of pasture or cropping land. Many ground layer species have been lost altogether (Romanin *et al.* 2016) or relegated to corners of old cemeteries or thin strips of roadside vegetation, free from the trampling hooves of introduced stock (Kirkpatrick *et al.* 1988; Prober and Thiele 1995; Department of the Environment Water Heritage and the Arts 2010).

Further, there is widespread mortality of adult trees in grassy eucalypt woodlands, a syndrome called 'rural tree decline' or 'rural dieback' (Landsberg 1990; Jurskis 2005). Under natural conditions, woodland eucalypts are well adapted to drought, but when stressed by competition with exotic pasture grasses, soil compaction and nutrient enrichment from fertilisers, they are vulnerable to drought and insect attack (Landsberg and Wylie 1988; Landsberg 1990; Neyland 1999; Close and Davidson 2004; Jurskis 2005). Trees in poor health produce little or no seed, and seedling establishment is inhibited by the absence of natural disturbance regimes that include fire and native marsupial digging (Landsberg and Wylie 1988; Neyland 1999; Close and Davidson 2004; Jurskis 2005). Those seeds that do germinate are then threatened at seedling, sapling and pole stages by damage caused by native marsupials, stock animals, and in some regions, large numbers of exotic feral herbivores, particularly rabbits and deer (Semple and Koen 2001; Keith and Pellow 2005). Many paddock trees are reaching the end of their lifespans, which, when coupled with a shortage of natural eucalypt regeneration, makes the persistence of these relictual patches unlikely into the future (Reid and Landsberg 2000; Dorrough and Moxham 2005).

In primarily privately-owned landscapes, such as the Tasmanian Midlands, the conservation of native vegetation does not fit the model of public funded conservation areas such as national parks and nature reserves (henceforth we called 'public conservation'). Public conservation in the Midlands is restricted because areas of intact vegetation on public land are limited in extent and do not represent the full range of ecological complexes. Moreover, landowners are generally unwilling to sell small remnant patches of native vegetation, particularly areas with fertile soils that have often been sown with exotic pasture grasses. Consequently, only 1–2 % of the Midlands bioregion is currently protected by public conservation reserves (Males 2009; Cowell *et al.* 2013). Exacerbating the situation, native vegetation on flat, fertile land is not effectively reserved and the remaining areas are declining as agricultural intensification increases (Lunt 1991; Pressey and Logan 1997; Iftekhar *et al.* 2014). However, management agreements between the government and non-government organisations can protect high conservation private lands outside the public conservation estate (henceforth we call 'private conservation'), thereby complementing the existing public reserve system (Fitzsimons and Wescott 2001; Fischer *et al.* 2011). It is important to note that such small private conservation reserves are critical stepping stones for wildlife, which can increase connectedness between larger areas of native vegetation that surround agricultural areas (Pressey and Logan 1997).

Over the last two decades there has been an expanding private conservation network in Tasmania (Fig 1b.). For instance, in 1997 the Tasmanian Regional Forest Agreement set up a Private Forest Reserves Program to protect forest communities that are under-reserved on public land (Syneca consulting 2007). Soon afterward, in 2003, the State Government enacted the Non-Forest Vegetation Project which began working with Midlands landowners to protect areas of grassy woodland with conservation covenants (Cowell *et al.* 2013). These covenants are voluntarily agreed upon between the landowner and an authorised body, and have become a common way of preserving native vegetation on private land (Natural Resource Management Ministerial Council 2009; Putten *et al.* 2011). Covenants are usually enacted for perpetuity and the landowner may receive tax concessions as well as assistance with fencing and weed control (Burns *et al.* 2016). In addition to the above government private conservation schemes, non-government organisations organise a range of conservation agreements to protect and manage vegetation

with high conservation value on private land in Tasmania (Males 2009; Iftekhar *et al.* 2014). Finally, some landowners voluntarily designate areas as private reserves in an informal manner. Typically, land owners retain the right to graze private conservation areas, albeit at stocking rates considered sympathetic to biodiversity conservation, whereas grazing is typically discouraged or actively excluded from public conservation reserves.

The efficacy of public and private conservation reserves in ensuring the persistence of trees in the landscape remains poorly studied (Iftekhar *et al.* 2014). It is challenging to interpret research findings because reserves on public land have often experienced a different suite of historic land use disturbances compared to those on areas of private property now managed for conservation. Here, we examine the demographics of the most abundant overstorey species of *Eucalyptus* woodlands in public and private conservation reserves. For conservation areas to be effective, they should foster sufficient recruitment of *Eucalyptus* and other tree species to maintain a healthy overstorey. Under favourable herbivore and fire disturbance regimes overstorey species will recruit frequently, whereas a disruption to recruitment will cause an absence of seedlings or juveniles, and over the long term, imperil tree populations (Prior *et al.* 2011). Overstorey recruitment dynamics can also be affected by changes to the ground layer vegetation (Semple and Koen 2003); for instance 'improvement' for agriculture with exotic grasses can negatively influence *Eucalyptus* regeneration, and areas with a longer history of agriculture tend to have a higher proportion of both pasture grasses and exotic weed species.

The purpose of this study is to examine the effectiveness of conservation reserves in the Tasmanian Midlands and, in particular, whether important native species, particularly eucalypts, are successfully regenerating in these reserves. To do this we compared the population structures of the most abundant native tree species in both public and private conservation reserves with those in relatively undisturbed native vegetation, which are likely to have frequent tree regeneration, and in pastures still grazed for livestock production, where there is typically little tree regeneration. A trend of increasing tree regeneration in recent years would indicate that conservation reserves have been locally effective in reversing the population declines prevalent in the region. We also measured the composition of ground

layer vegetation. The cover of exotic weeds and pasture grasses is typically highest in areas which have been used for livestock production and these can inhibit recruitment of overstorey seedlings through their competitive effects. Knowing the persistence of such species after removal of grazing can therefore help understand patterns of tree regeneration, and the factors that limit it.

Methods

Geographical context and study design

The lowland (< 300 m asl) Midlands region occupies a north to south orientated graben, which divides Tasmania's Central Plateau from the Eastern Tiers. The regional climate is classified as temperate with warm summer (Cfb) according to Köppen-Geiger classification (Peel *et al.* 2007). A topographic rain shadow makes the Midlands the driest part of Tasmania (Fensham 1989) with approximately 500 mm mean annual precipitation, distributed evenly throughout the year (Fig. 1a). Frost may occur during any month of the year with an average of 100 frost days annually (Bureau of Meteorology 2008). The geology of the region is varied, and includes dolerite, basalt, sandstones, and some areas of sediments intensely weathered in the Cainozoic to form laterites (Brown *et al.* 2012). The original vegetation was a mosaic of lowland grasslands, grassy eucalypt woodland and dry eucalypt forest (Fensham 1989). It is postulated that fire was important in the evolution and maintenance of the vegetation communities of the Midlands (Thomas and Hope 1994; Harris and Kitchener 2016; Romanin *et al.* 2016).

The Midlands is one of the most highly modified agricultural areas of Australia (Barson *et al.* 2000; Close and Davidson 2004) and is 98% privately owned (Cowell *et al.* 2013). The average size of agricultural holdings in the Midlands is much larger than the Tasmanian average (1,750 ha compared with 405 ha) (Gadsby *et al.* 2013). The first European settlers in the early 19th Century targeted grasslands and grassy woodlands on the more productive soil, often derived from basalt (Matthews 1983), for sheep grazing. By 1940 most of the good lowland grazing land was under agricultural production (Kirkpatrick 2007a), thus, native vegetation types found on flat and fertile soils have vanished, with the only surviving native element being scattered paddock trees (Gilfedder and Kirkpatrick 1997; Ozolins *et al.* 2001; Gibbons and Boak 2002). Continuing intensification of agriculture, particularly large scale irrigation and cropping, means that these

remnants are under threat from 'secondary tree clearing' (Prior *et al.* 2013). The remaining area of native grassland and grassy woodland is small and largely restricted to undulating terrain with less fertile soils on private land. These native pastures were initially maintained by graziers through controlled burning to create green pick, but since the 1930s large areas have been modified by pasture improvements including ploughing, application of superphosphate, and the establishment of subterranean clover (*Trifolium subterraneum* L.) and exotic pasture grass species such as ryegrass (*Lolium* spp.) and *Bromus* spp. (Kirkpatrick 2007a). Correspondingly, the extent of native grasslands has sharply declined and there are no entirely undisturbed areas remaining. For instance, communities dominated by the tall C_4 grass, *Themeda triandra* Forssk. have been invaded by exotic species following the application of fertilisers that increase the agricultural productivity of these systems but decrease the growth of the native dominant grass (Groves *et al.* 2003). Forest and woodland on inaccessible, steeper or less productive terrain were used less intensively, and subjected mainly to seasonal or light stocking of sheep and low intensity firewood and fencepost harvesting, meaning they remain close to their natural state.

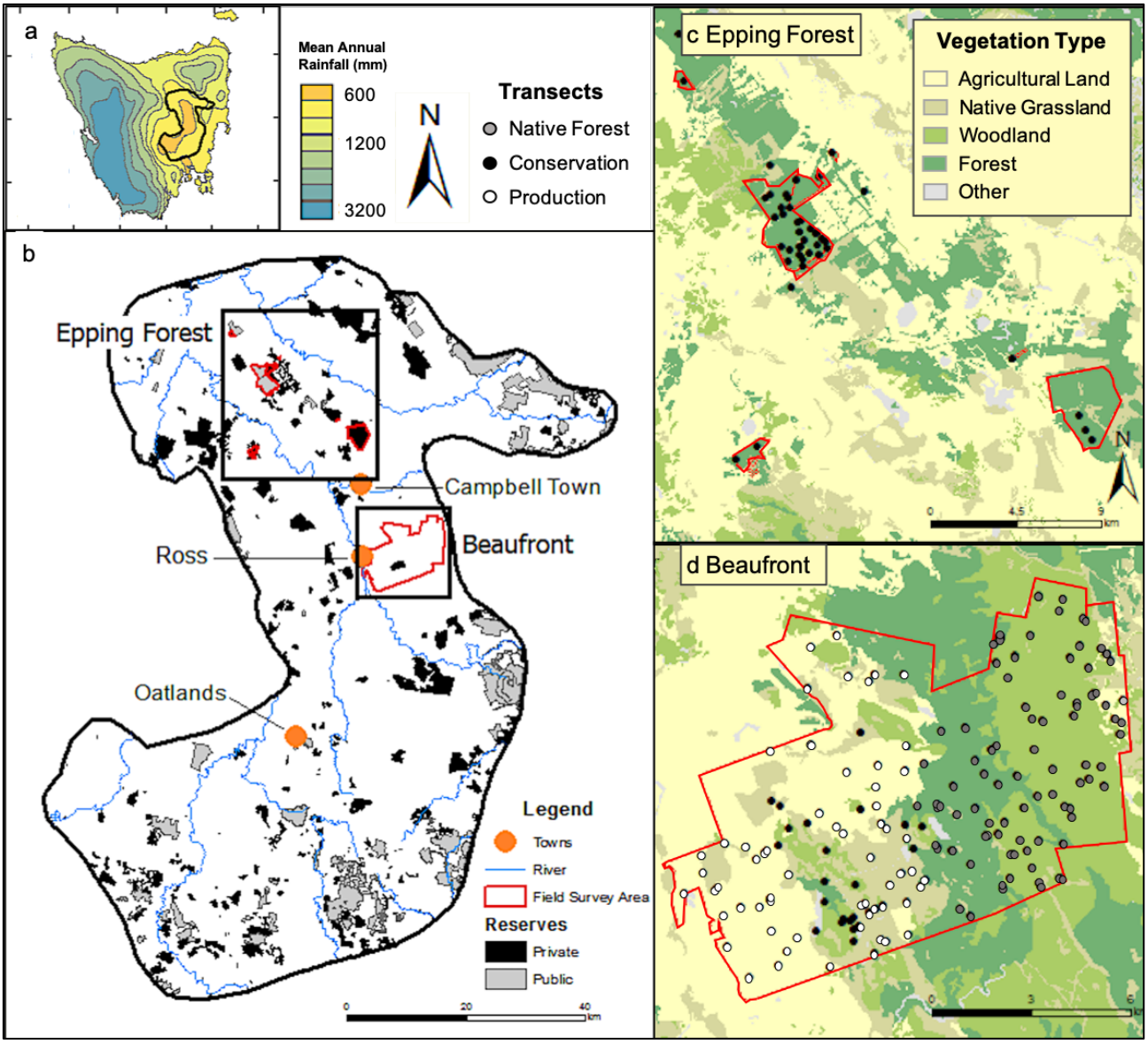

Fig 1. Study area in the Tasmanian Midlands. (a) Map of Tasmania showing rainfall isohyets (mm) and the Tasmanian Midlands Biodiversity Hotspot (outlined). (b) Conservation reserves, private (dark grey) and public government (pale grey) in the Tasmanian Midlands Biodiversity Hotspot. Epping Forest and Beaufront study areas are delineated in the black rectangles and enlarged in (c) and (d). (c) The boundaries of the Epping Forest sampling areas (red) include four small private conservation covenants and one larger public reserve (Tom Gibson Reserve). (d) The Beaufront study area (red) is a large privately owned agricultural property. Dots are individual transects; Native Forest (grey), Conservation (black) and Production areas (white). The boundary of the Midlands Biodiversity Hotspot was provided by M. Taylor and S. Bryant (Tasmanian Land Conservancy).

Field sites, land-types and their land use histories

This study focusses on two sites: Beaufront and Epping Forest These sites have contrasting environments and a variety of land uses, as outlined below. The Beaufront site is one large (12,500 ha) privately owned property, south of Ross (Lefroy 2011) (Figs. 1b & 1d). The Epping Forest site was once a continuous forest

that is now highly fragmented, and includes one small public (1,020 ha) and several private (most <5 ha) conservation reserves (Figs. 1b & 1c).

Beaufront includes diverse vegetation types and land use practices characteristic of the Midlands. Fertile soils derived from basalt and dolerite have been preferentially cleared, while native vegetation on rocky sites and soils derived from sandstone remains relatively intact. The property is broadly divided into production (livestock and cropping) and intact vegetation. Areas used for cropping were not considered in our study as they had no likelihood of tree regeneration. The vegetation on the property ranges from *Eucalyptus* forests and open grassy woodlands dominated by *Eucalyptus amygdalina* Labill., *Eucalyptus pauciflora* Sieber ex Spreng. and *Eucalyptus viminalis* Labill. to native grassland complexes (Harris and Kitchener 2016) (Tabulated in Appendix 1). To inform the land-type classification and hence field sampling strategy and interpretation of findings, two generations of landowners were interviewed to obtain a land use history of Beaufront (Ethics approval ref. H0013287). Information on land use, grazing and fire history are described below and summarised in Table 1.

Epping Forest, in the northern part of the Midlands, was typically *Eucalyptus amygdalina* inland woodland or forest, strongly associated with the low fertility, Cainozoic lateritic sediments distinctive of this area (Harris and Kitchener 2016) (Appendix 1). The structure of this vegetation complex is highly influenced by fire and land use history and has a variable ground layer comprised of shrubs, bracken fern (*Pteridium esculentum* (G.Forst.) Cockayne) or grasses. This vegetation type remained uncleared until the 1970s, when correcting for trace element deficiencies in soils became possible (Fensham 1991; Kirkpatrick 2007a) and there were financial incentives to convert forest to pasture (Prevost 1988). Epping Forest is now highly fragmented with less than 14% of its former extent remaining (Lefroy 2011).

Our analysis is organised according to the broad categories of Native Forest, Conservation and Production areas. Various combinations of site and land uses are present, which we term *land-types*, as described below. In testing the questions outlined in the introduction, we considered Native Forest to be land-type Native Forest (Beaufront), Conservation reserves to be land-types Private Conservation (Beaufront &

Epping Forest), and Public Conservation (Epping Forest), and Production areas to be land-types Rangeland (Beaufront) and Improved Pasture (Beaufront).

Native forest

Native Forest (Beaufront)

The Native Forest land-type on Beaufront is unreserved but only minimally modified. The Native Forest was lightly grazed in the past, but land owners have excluded sheep from the area for over 10 years (Table 1). It has a history of firewood and fencepost extraction, and some areas were logged for woodchips between 1960 and 1980. Native Forest sites were burned at a 3-4 year fire return interval by the land owners until approximately 2003 (Table 1).

Conservation reserves

Public conservation - Tom Gibson Reserve (Epping Forest)

Public conservation in the Northern Midlands consists of one formal reserve, Tom Gibson Reserve, a 1020 ha public nature reserve, established by the Tasmanian state government in 1991. The Tom Gibson Reserve management plan permits grazing year-round by 300 sheep, but actual numbers are much lower than this (Parks and Wildlife Service Tasmania 2006). Prior to 1991, the Reserve was mined for gravel and more heavily stocked with sheep. Regular controlled patch burning has been reinstated at the Reserve (Gilfedder and Kirkpatrick 1998; Tasmania Fire Service 2017).

Private Conservation (Epping Forest)

The Private Conservation transects in Epping Forest were distributed amongst several private properties. They are on perpetual conservation covenants established between 2000 and 2008. There is scant information about the grazing and fire history in the Epping Forest area, although it is known that intense wild fires burnt some areas in 2008-11 (Tasmania Fire Service 2017) and 2013 (Prior *et al.* 2016).

Private Conservation (Beaufront)

The Beaufront Private Conservation reserves have had no stock grazing for 20 to 30 years but are within a matrix of agriculturally productive land. This land-type has never been ploughed but was aerially top-dressed with subterranean clover (*Trifolium subterraneum*) and super phosphate, and other exotic pasture species have established in some areas. Beaufront Private Conservation reserves have not been regularly burned since the 1960s (Table 1).

Production areas

Rangeland (Beaufront)

Rangelands on Beaufront include some abandoned agricultural land (DPIPWE 2009) with remnant paddock trees. In order to preserve environmental values of these areas, the Rangelands are stocked with sheep only during lambing periods because the native tussock species, such as *Poa labillardierei* Steud. and *Lomandra longifolia* Labill.*,* provide shelter for newly born lambs. Most Rangeland areas have never been ploughed but have been aerially top-dressed with subterranean clover (*Trifolium subterraneum*) and superphosphate. Other exotic pasture species have also been established on some Rangeland areas (Table 1). The Rangelands were burned at a 3-4 year fire return interval by the land owners until approximately 2003 (Table 1). In attempts to reinstate historic fire regimes, small patch fires were lit during 2013 in some Rangeland areas.

Improved Pasture (Beaufront)

Improved Pasture on Beaufront has a long history of sheep grazing that is ongoing and intensive (Table 1). Areas with Improved Pastures are mostly on basalt substrates (Appendix 1) and are found close to roads and homesteads. Beginning in the 1930s, exotic pasture species have been planted, large areas have been ploughed and fertiliser application is regular. Only very small areas (< 3 ha) of native grassland remain in Improved areas. Improved Pastures have experienced no regular fire since the 1960s because the threat of litigation made many land owners unwilling to risk damage to neighbouring property attributable to escaping fire (Table 1).

Table 1. Historic land use practices for each of the land-type categories used in this study.
Fire history is defined as the historic fire return interval (FRI) and was estimated from landowner interviews. **+** indicates light strategic grazing, ++ for productive grazing, • indicates intentional efforts to improve pastures, **-** indicates absence, 'n.a.' indicates no information. Current grazing at Rangeland and Epping Forest Public Conservation is light or periodic. Last fire date is relative to data collection which ended in 2014; some areas have burned since then. Data collated from a landowner interview and a fire history dataset (ListMap). n is number of transects. Land-type codes are: B-F – Beaufront Native Forest; EF-TG– Epping Forest Public Conservation; EF-PC – Epping Forest Private Conservation; B-PC – Beaufront Private Conservation; B-R –Beaufront Rangeland; B-IP – Beaufront Improved Pasture

	Land-type	*n*	Past grazing	Current grazing	Introduced pasture	Fire history (FRI)	Last fire
Native Forest	B-NF	52	+	-	-	3-4 year	2003
Conservation Reserves	EF-TG	26	+	+	-	n.a.	2011
	EF-PC	15	+	-	-	n.a.	2008-09
	B-PC	20	++	-	•	long unburnt	n.a.
Production Areas	B-R	46	++	+	•	3-4 year	2013
	B-IP	21	++	++	•	long unburnt	1960s

Field-based measurements

Field sampling was based on 180 belt transects that were randomly selected from the Beaufront (139) and Epping Forest (41) areas using ArcGIS 10 (ESRI, Redlands, CA) and 2012 satellite imagery. The position of the centre of each transect was located using a GPS. The transects were 50 m long and 20 m wide and ran either north-south or east-west, randomly decided by a toss of a coin. These transects were categorised according to current land-type category. At Beaufront and Epping Forest we established 52 transects in Native Forest, 61 transects in Conservation reserves (26 public, 35 private) and 67 transects in Production areas (Table 1).

Tree size class structures in each 1000 m^2 transect were measured to provide an indication of tree recruitment dynamics (Prior et al. 2011). The diameter at breast height (DBH) of all live trees (defined as >5 cm DBH) and saplings (defined as >1.5 m tall and <5 cm DBH) was measured. All trees were scored as alive or dead. Live stand basal area was calculated as the sum of the basal area of individual live trees.

The number of *Eucalyptus* and other species' seedlings <1.5 m tall were counted within 2 m of the centre line of the transect (an area of 200 m^2). *Acacia* seedlings were counted within 1 m of the centre line of the transect (a smaller area of 100 m^2 was used because where present, their numbers were very high). No seedlings were found at Improved Pastures, therefore this land-type was excluded from further seedling analysis. Trees and seedlings were identified to species level wherever possible; the identity of *Eucalyptus* seedlings was inferred from the overstorey species in a stand.

The ground layer was evaluated within a 1 x 1 m quadrat at six locations along the midline of 130 transects; a small number of sites with a shrubby ground layer at Beaufront were excluded. Tree demographic data from Epping Forest private conservation reserves were collected as part of another study, and ground layer data were not collected for these transects. The percent cover of native grass and forbs, exotic pasture species, litter, moss, rock and bare ground was recorded. This percent cover could sum to more than 100% where layers of ground cover overlapped. Average cover for each component was calculated for each transect. We also measured woody debris in each 50 m transect, as it forms an important structural component of many Australian ecosystems and can provide safe sites for seedling establishment (Enright and Lamont 1989; Davidson *et al.* 2007; Bailey *et al.* 2012). We used the line intersect sampling method to measure the diameter of all woody debris (>1 cm) that crossed the midline of each transect. The volume of woody debris per hectare was calculated for each transect using the equation:

$$WD = \frac{\pi^2}{8L} \times \sum_{i=1}^{n} d_i^2$$

where WD is the volume of woody debris (m^3 ha^{-1}), L is transect length (m) and d_i is the diameter of the ith branch or log (cm) (Marshall *et al.* 2000).

Analyses

Our statistical approach was to use multi-model inference combined with model selection using Akaike's Information Criterion adjusted for a small sample size (AIC_c) (Burnham *et al.* 2004). Low values of

AIC_c indicate strong support, and we considered a difference in AIC of >2 statistically important (Burnham *et al.* 2004).

All statistical analyses were conducted using the using the R statistical package (R Core Team 2017). The glmmADMB (Skaug *et al.* 2016) package was used to calculate the negative binomial regression as it can include random effects. To calculate the difference between different models and to return model weights (w_i) the bbmle package (Bolker and R Development Core Team 2017) was used. The PCA of ground layer components was plotted using the ggbiplot package (Vu 2011). The PerformanceAnalytics package (Peterson and Carl 2014) was used to plot the correlation matrix and calculate Spearman's rank coefficients.

We examined whether there were differences in stand structures, proportion of veteran trees, seedling density and ground layer composition among the land-types defined above. The 21 transects established on Improved Pastures were not used in the statistical analysis of stand structures or veteran trees because only one transect retained trees, leaving a total of 159 transects for analysis.

We examined the effects of land-type on stand structures of the four most abundant tree species, namely *Eucalyptus viminalis* Labill., *Eucalyptus amygdalina* Sieber ex Spreng., *Acacia dealbata* Link and *Banksia marginata* Cav. Conformation to a negative exponential stand structure suggests a stand has reasonably constant rates of recruitment, growth and mortality across size classes (Rubin *et al.* 2006). All live trees >1.5 m high were grouped into 10 cm-DBH size classes (SC), specified by the DBH of the midpoint of the SC. First, we tested whether the count-size class relationship varied among land-types using a negative binomial generalised linear model with transect as a random effect to account for spatial autocorrelation, and SC*land-type as potential explanatory variables. For each of the abundant species there was evidence of differences among land-types (AICc of the SC*land-type model was lower than that of the null model (Appendix 2)). We then investigated whether populations of these species within each land-type conformed to a negative exponential distribution by fitting the size-class model for each species – land-type combination separately (Rubin *et al.* 2006; Prior *et al.* 2011), comparing the count-SC model with the null model. If the AIC of the null model minus AIC_c of the count-SC model was >2, w+ greater than 0.73

and the slope was negative, we considered the stand structure approximately conformed to a negative exponential distribution. A positive slope was considered an indicator of poor recruitment in recent years.

Large, veteran trees are keystone structures in agricultural landscapes, providing habitat and ecosystem services (Manning *et al.* 2006), but an over-representation of this size class denotes senescing stands unlikely to replace themselves due to low fecundity. We therefore examined whether the proportion of the total *Eucalyptus* basal area was accounted for by trees over 80 cm DBH and varied among the five land-types by comparing binomial generalised linear models with and without land-type as an explanatory variable.

Seedlings and saplings were analysed separately, grouped according to the three genera, *Eucalyptus*, *Acacia* and *Banksia*. Negative binomial glms (which accounted for over-dispersion in the data) were used to test whether seedling counts varied among land-types for each genus. The land-type models were compared against null models using AIC_c.

To explore patterns in ground layer composition across the land-types a principal components analysis (PCA) was performed, with the data scaled and centred.

Results

This study found that land-use history profoundly affected tree population demographics in the Tasmanian Midlands. Native forests and the conservation reserves at Epping Forest, had demographically sound populations of overstorey tree taxa and a ground layer composed of primarily native species. Private Conservation land-types at Beaufront had apparently unsustainable tree demographics and ground layers comprised of native and exotic grass species. 'Production' areas also had unsustainable tree demographics, with Improved Pasture land-types transformed to almost completely exotic vegetation. These contrasting patterns in ground cover and tree demographics are described below.

Abundant species

Eucalyptus species were the most abundant overstorey trees across the whole area. *Acacia* was the most abundant midstorey genus, and in some areas these trees were more common than *Eucalyptus*. *Banksia marginata* was an abundant structural element at Epping Forest only.

The most abundant *Eucalyptus* species across the entire Beaufront site was *E. viminalis*; it was present at the most transects under all land-types (a full list of tree species is included in Appendix 3). By contrast, *E. amygdalina* was the most abundant eucalypt of the Epping Forest sites, occurring on 23 of 26 Public Conservation (EF-TG) and 14 of 15 Private Conservation (EF-PC) transects and at much higher density than *E. viminalis*.

Midstorey tree taxa varied considerably between land-types (Appendix 3). *Acacia dealbata* was found at high densities across all land-types and was found in 76% of transects in Native Forest and Epping Forest conservation land-types (Appendix 3). In the Epping Forest site, *Banksia marginata* was found at approximately 50% of transects. However, *B. marginata* was rare at the Beaufront site, and only found at Native Forest (2 of 52 transects) and Rangeland (2 of 46 transects).

Proportion of trees alive

The Native Forest (Beaufront) land-type had the greatest proportion of live trees, which were found at most plots; *Acacia* (80%), *Eucalyptus* (73%) and all species combined (77%) (Table 2). Most plots at conservation land-types (Epping Forest land-types) also had live *Acacia* and *Eucalyptus*. Between 87% and 100% of plots at Native Forest and Epping Forest conservation land-types had live *Acacia* and *Eucalyptus*. By contrast the number of plots and proportion of live *Eucalyptus* was low at conservation and production land-types at Beaufront (Improved Pasture, Rangeland and Private Conservation) (Appendix 3). Rangeland had the lowest proportion (31%) of live *Eucalyptus* stems and in Improved Pasture, live trees were only found at only one transect (Table 2). The lowest proportion of live *Acacia* was at Private Conservation sites in Epping Forest (40%); this may reflect the short life span of *Acacia* and a lack of recent disturbance.

Table 2. Live tree density (mean ± s.e.) and percent alive of most abundant tree genera and all woody species combined across all land-types except improved pasture. Density for 'all *Acacia*', 'all *Eucalyptus*' and 'all species' are averaged over all plots whether or not present in that plot. *n* (total) indicates the number of plots at which live trees were found, with total plots at that land-type in parentheses. Percent alive is only presented for 'all acacias', 'all eucalypts' and 'all species' as trees could not reliably be identified to species when dead. Land-type codes are: B-F – Beaufront Native Forest; EF-TG – Epping Forest Public Conservation; EF-PC – Epping Forest Private Conservation; B-PC – Beaufront Private Conservation; B-R –Beaufront Rangeland. Improved Pasture land-type is excluded as the only trees at this land-type were 13 live *E. viminalis* trees, all at one transect.

Land use category	Land Type	all *Acacia*			all *Eucalyptus*			all species		
		Alive (%)	*n* (total)	Density (ha^{-1})	Alive (%)	*n* (total)	Density (ha^{-1})	Alive (%)	*n* (total)	Density (ha^{-1})
Native Forest	B-NF	79.7	41 (52)	346 (±63)	73.3	42 (52)	200(±41)	77.4	45 (52)	556(±88)
Conservation	EF-TG	50.1	24 (26)	145(±26)	70.8	23 (26)	145 (±17)	60.2	24 (26)	387 (±48)
	EF-PC	39.6	15 (15)	190 (±37)	62.3	15 (15)	169 (±21)	55.9	15 (15)	525 (±81)
	B-PC	77.5	5 (20)	338 (±102)	55.1	10 (20)	22 (±7)	71.6	13 (20)	107 (±57)
Production	B-R	84.6	14 (46)	36 (±23)	31.1	9 (46)	7 (±3)	65.9	19 (46)	44 (±24)

Stand structure

The native forest showed frequent regeneration of all four major species, with populations of *E. viminalis*, *E. amygdalina* and *A. dealbata* conforming to a negative exponential distribution (Fig. 2). There were high densities of *B. marginata* juveniles, but no large trees. Frequent regeneration of all four species, and negative exponential population structures, were also evident at two of the three 'conservation' land types. However, at Beaufront conservation, only *A. dealbata* populations conformed to a negative exponential distribution, and there were no small adult (or juvenile) eucalypts. Similarly, there were few small eucalypts at the two 'production' land-types. In the Beaufront rangeland, there were low-moderate densities of *E. viminalis* trees >20 cm DBH, but none smaller than this. There were no *E. amygdalina* trees, and very few *B. marginata* ones (Fig. 2). On Improved Pastures, only one of the 21 transects retained any trees, and these were all in the medium size classes.

Veteran trees

Native Forest and conservation land-types (Epping Forest) had the lowest proportion of large trees. Rangeland and Beaufront private conservation land-types had high proportions of veteran trees (66% and 57% respectively) compared to ~35% in Native Forest and two of the three conservation land-types; but an overall difference among the land-types was not supported statistically (w+=0.12) (Table 3)

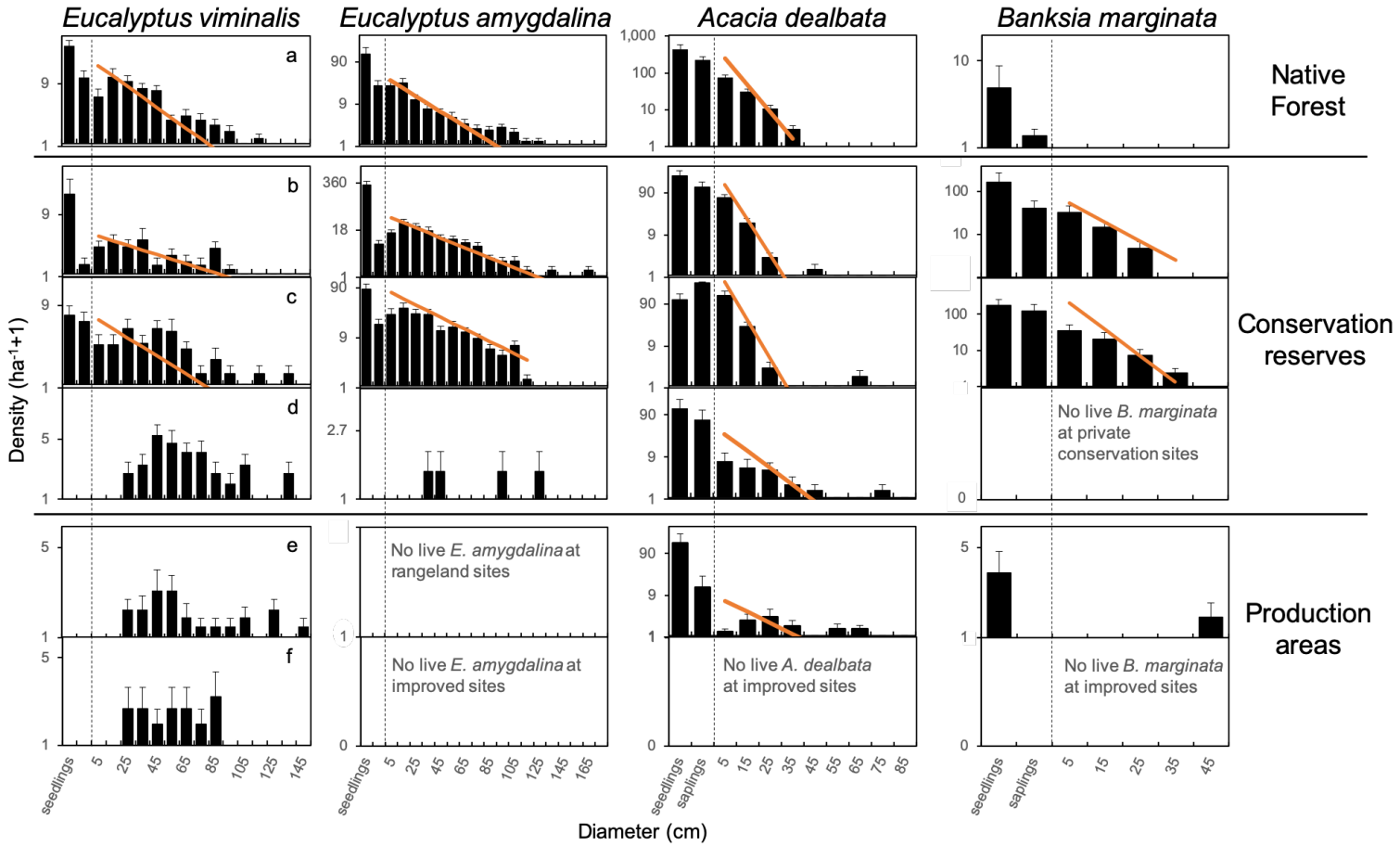

Fig. 1. Density (mean ± s.e.) of live *Eucalyptus amygdalina*, *Eucalyptus viminalis*, *Acacia dealbata* and *Banksia marginata* trees as a function of diameter, note the log scale on the y-axis. Trees were binned into 10-cm diameter classes, the midpoint of each is presented. The zero to 10cm class was divided into saplings (>1.5m high to <5cm DBH) and small trees (>5 to <10cm DBH). Seedlings (<1.5cm high) were counted on each transect but not included in statistical modelling. The orange lines indicate approximate fit to a negative binomial distribution. Beaufront Conservation, Rangeland and Improved Pasture land-types had no individuals in the smallest size classes. No *E. amygdalina* individuals were found in Rangeland or Improved Pasture land-types. *Banksia marginata* was very rare on the Beaufront site. The land-type categories examined are (from top to bottom): a. Native Forest (Beaufront); Conservation reserves – b. Tom Gibson Reserve (Epping Forest), c. Private Conservation (Epping Forest), d. Private Conservation (Beaufront); Production Areas – e. Rangeland (Beaufront) and Improved Pasture (Beaufront) The land-types have been arranged based on expected regeneration success. Note the scale on the y-axis differs amongst graphs.

Table 3. Mean live eucalypt basal area, proportion of veteran Eucalyptus (>80cm DBH) basal area, *Eucalyptus* seedling density and canopy cover for each of the land-type categories used in this study.
Standard error is presented in parentheses. Land-type codes are: B-F – Beaufront Native Forest; EF-TG – Epping Forest Public Conservation; EF-PC – Epping Forest Private Conservation; B-PC – Beaufront Private Conservation; B-R – Beaufront Rangeland; B-IP – Beaufront Improved Pasture. Note, canopy cover data were not collected at EF-PC land-types, 'n.a.' indicates no information.

	Land-type	Total basal area	Veteran basal area	Seedling density	Canopy cover
		$m^2\ ha^{-1}$	%	$Stems\ ha^{-1}$	%
Native forest	B-NF	14.6 (±1.8)	35.0	247 (±73.7)	90.1
Conservation	EF-TG	20.4 (±2.8)	36.9	386 (±87.0)	97.7
	EF-PC	24.2 (±1.9)	38.3	177 (±49.0)	n.a.
	B-PC	8.6 (±2.5)	57.0	3 (±2.5)	57.2
Production	B-R	2.8 (±1.1)	66.4	8 (±5.4)	34.8
	B-IP	1.8 (±1.8)	45.6	0	6.6

Juvenile density and species diversity

Acacia seedling density was much higher than *Eucalyptus* under every land-type category, indicating its role as a pioneer species. Land-type was a good predictor of seedling density for the three genera examined (Appendix 4; $w_i = 1.00$). The largest areas of intact vegetation (Native Forest and Tom Gibson reserve) supported the highest overall numbers of seedlings (Appendix 5; Native Forest, 1018 ± 34 stems ha^{-1}, Tom Gibson Conservation, 1019 ± 59 stems ha^{-1}). Among the land-types, seedling species diversity was highest at Native Forest, with 15 species found (Appendix 5). *Acacia* seedling density was highest in Native Forest. The density of *Eucalyptus* seedlings was highest at Tom Gibson Reserve (386 ± 87 stems ha^{-1}). *Eucalyptus* seedling density was lower at Epping Forest Private Conservation (177 ± 49 stems ha^{-1}) and seedlings were almost absent from Beaufront Private Conservation (3 ± 2.5 stems ha^{-1}). The lowest density of *Acacia* seedlings was also found at Beaufront Private Conservation (3 ± 2.5 stems ha^{-1}) (Appendix 5). *Banksia* seedlings were found at the greatest proportion of transects in the two conservation land-types in Epping Forest, which are geographically close. Production areas also had low rates of regeneration, and there were no seedlings of any species at Improved Pasture sites.

Land-type was a good predictor of sapling density for the three genera examined (Appendix 6; $w_i = 1.00$). *Eucalyptus* sapling density was highest at Native Forest (5 ± 1.3 stems ha^{-1}) and Tom Gibson Reserve (3 ± 0.7 stems ha^{-1}). *Banksia* saplings were most abundant at the Epping Forest land-types. No *Eucalyptus* saplings were found at Beaufront Private Conservation and *Acacia* saplings were growing in just two transects at this land-type. No saplings of any species were found at Improved Pasture sites.

Ground cover

There were marked differences between the land-types for all of the ground layer components (Fig. 3 & Table 4). Native Forest and Tom Gibson conservation reserve had the highest cover of native grasses (68%) and litter (Native Forest – 30%, Tom Gibson Reserve – 38%). Additionally, the volume of woody debris per hectare was highest at these land-types. While the Native Forest land-type had not been intentionally planted with exotic pasture species, an average of 7% exotic cover was found at these sites. Public conservation at Epping Forest (Tom Gibson Reserve) had almost no exotic pasture cover and was statistically different from each of the other land-types (Table 4). Litter and woody debris were lowest at the 'production' land-type, Improved Pasture: litter by one order of magnitude and woody debris by two orders of magnitude (Table 4).

The first axis of the PCA (PC1) of ground layer attributes described a spectrum of native *vs* exotic cover explaining 42% of the variation, while the second axis (PC2) explained a further 19% by segregating transects according to rock cover and bare ground (Fig. 3). The Native Forest and Tom Gibson Reserve transects were associated with high cover of native grasses and forbs and litter, while all Improved Pasture transects clustered together at the opposite end of the ordination space, commensurate with their high exotic cover. Private conservation and Rangeland transects at Beaufront were intermediate between these extremes, with a mix of native grasses and exotic pasture species (Table 4) and high variability in cover between sites as demonstrated in the PCA (Fig. 3). The tight overlap of litter and native grass/forb vectors indicates a strong correlation between these ground layer components (Fig. 3).

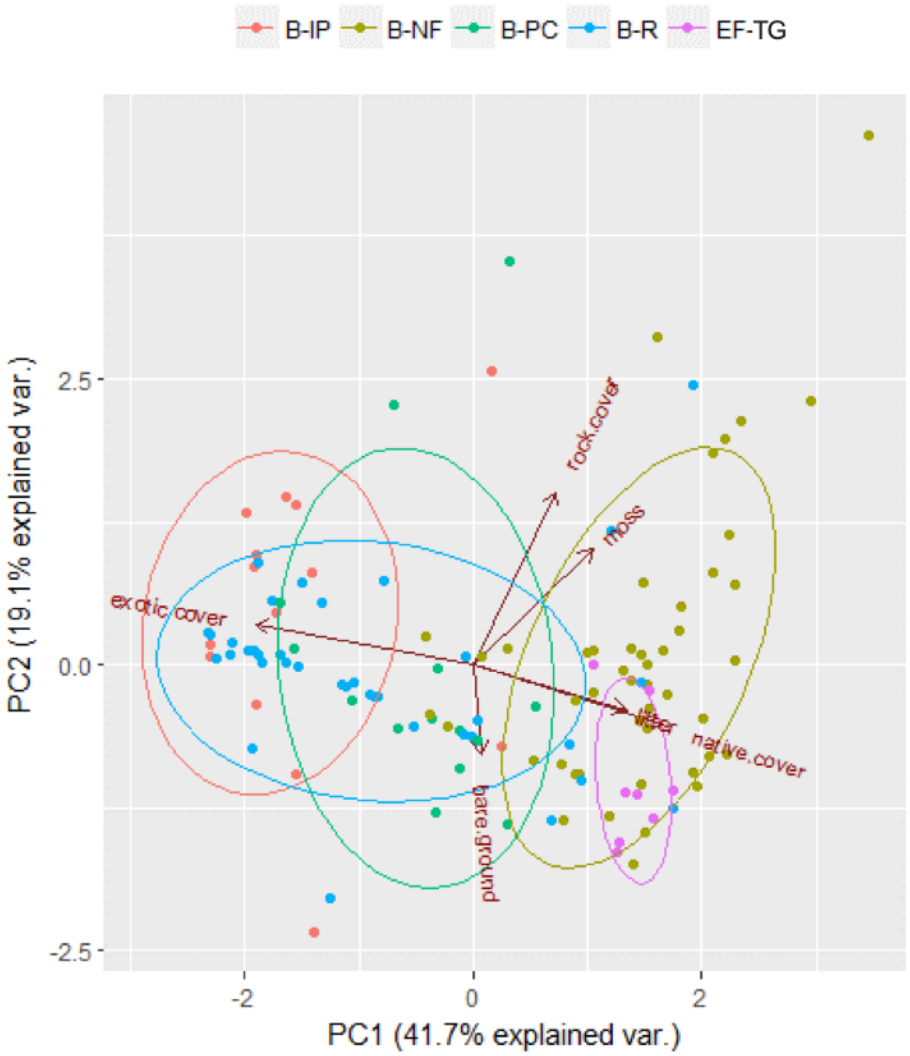

Fig. 2. Principal components analysis (PCA) relating ground cover components to land-type categories. The clusters of Beaufront Native Forest (B-NF), Epping Forest Public Conservation (EF-TG), Beaufront Private Conservation (B-PC), Rangeland (B-R) and Improved (B-IP) transects are outlined. The loadings explaining most of the variation in PC1 are: exotic cover(-0.607), native cover (+0.531), and litter (+0.429). The loadings with the most explanatory power in PC2 are: rock cover (+0.713), bare ground (-0.372) and native cover (-0.249). The loadings of the first two principal components explain 60% of the variation in the data.

Table 4. Mean ground cover and volume of woody debris (WD) for each of the land-type categories used in this study.

Note ground cover components could add to more than 100% cover at each site. n is the number of transects data were collected, and data were not collected at all sites and were not collected for the EF-PC land-types. Chi square values and p-values from Kruskal-Wallis tests performed for each ground cover variable. *** indicates p<0.001, ** indicates p=0.02. Mann-Whitney U-tests were used post-hoc to identify differences within each ground cover variable, land-types sharing the same letter are not significantly different. Land-type codes are; B-NF – Beaufront Native Forest, EF-TG – Epping Forest Public Conservation, EF-PC - Epping Forest Private Conservation, B-PC – Beaufront Private Conservation, B-R – Beaufront Rangeland, B-IP – Beaufront Improved pasture. 'n.a.' indicates no information.

site	Land-type	n	Exotic pasture species	Native grass/forb	Litter	Rock cover	Moss	Bare ground	WD
units			%	%	%	%	%	%	$m^3\ ha^{-1}$
Native Forest	B-NF	47	7.2^{b}	68.9^{b}	29.8^{b}	9.1^{b}	8^{b}	3.5^{b}	491
Conservation	EF-TG	8	0.3^{d}	68.4^{b}	38.4^{b}	3.7^{a}	3^{a}	9.1^{b}	355
	EF-PC	0	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
	B-PC	16	54.9^{c}	27.5^{c}	19.2^{b}	3.7^{a}	3.8^{a}	4.7^{ab}	113
Production	B-R	38	63.5^{c}	30.4^{c}	9.9^{c}	2.3^{a}	2.1^{a}	3^{a}	117
	B-IP	21	86.3^{a}	6.1^{a}	2.2^{a}	4.9^{a}	1.3^{a}	4.5^{a}	3
χ^2		df 4	90.6***	70.1 ***	53.0 ***	25.3 ***	29.2 ***	11.6 **	

Discussion

Our results highlight the legacy that land use history has on the persistence of trees in the landscape and on the composition of the ground layer. We found that private conservation reserves on Beaufront have declining populations of trees and current management practices, using very low stocking rates has failed to stimulate *Eucalyptus* recruitment. The areas little modified for agricultural production because of poor soils and rough, hilly terrain supported sustainable tree populations. Regeneration failure at Beaufront outside Native Forest areas appears linked to a long history of grazing, soil compaction, clearance of trees, fertilizer application and most particularly the introduction of exotic pasture grasses. Overall, our work suggests that differences in the original vegetation affect the persistence and health of remnant patches within the landscape, because vegetation type affects all of land-use histories and practices (Fensham *et al.* 1998; Romanin *et al.* 2015), regeneration potential and resilience to change. While we acknowledge that this study cannot disentangle the many factors at play in each of the land-types examined, we suggest land use history appears to have caused the landscape to shift to an alternative stable state that differs from the original vegetation (Prober *et al.* 2005). Restoration to the original vegetation state appears difficult once an ecological threshold has been crossed. This study adds to a body of work suggesting that removal of stock grazing does not necessarily result in a spontaneous recovery of grassy woodland vegetation (Clarke and Davison 2001; McIntyre *et al.* 2017). Below we elaborate this interpretation of our study.

Native Forest on Beaufront and conservation reserves at Epping Forest are reasonably large, intact areas with high native plant species richness (Gilfedder and Kirkpatrick 1998). These areas have the highest numbers of seedlings of all genera, and their tree stand structures are consistent with frequent recruitment of *Eucalyptus* and *Acacia* species. These had ground layers with high cover of leaf litter and native herbaceous species and low cover of exotic species, indicative of healthy ecosystem processes and soil nutrient cycles which are largely resistant to compositional change (McIntyre *et al.* 2017). Historical reconstructions show that Epping Forest and Native Forest

on Beaufront were naturally dense vegetation at the time of European arrival (Fensham 1989). These areas were used for seasonal grazing but were not extensively cleared or subjected to pasture improvement given the infertile soils at Epping Forest and shallow, rocky soils on slopes at Beaufront. The ecological health of these land-types is noteworthy given the past extractive land use, namely gravel mining at Epping Forest (Kirkpatrick 2007b) and firewood harvesting at Beaufront, as explained in the landowner interview. We observed differences in overstorey and midstorey species composition between the study sites. The cause of these differences in species composition could include soil type differences, the legacy of land-use history impacts or the differing resilience of the original vegetation, or a combination of all three. Overall, the demographic structure of both sites suggests woodlands will persist in the future under current management systems.

In contrast to the conservation reserves in the Epping Forest area, private conservation areas at Beaufront support only scattered or isolated *E. viminalis* trees and a handful of large *E. amygdalina* trees, all of which we can infer are old. For nearly 200 years prior to management for conservation, these remnants were used as shelter and fodder for sheep. These areas are located in a highly modified matrix of agricultural land, and fragmentation appears to have strongly negatively affected tree populations. Inclusion in the agricultural matrix means these areas have not undergone any patch burning for a long period. Patches are often distant from the next closest patch of native vegetation, which is often heavily modified, and most patches are very small. Despite being fenced off for conservation up to 30 years ago, there was no *Eucalyptus* recruitment in private conservation reserves. Thus we found, as have some other researchers, that fencing was not enough for maintaining overstorey tree populations (Lunt *et al.* 2000; Clarke and Davison 2001). However, in other studies, fencing of remnant vegetation to exclude stock did enhance regeneration of eucalypts and other tree species (Spooner *et al.* 2002; Briggs *et al.* 2008). Together, these findings suggest that grazing by domestic stock is an important constraint on tree regeneration in Australian temperate woodlands, but not the only one.

Seasonal grazing, as occurs in the rangeland land-type, is often employed to preserve native vegetation in a productive landscape. Light grazing occurs in winter and spring and is avoided in summer to allow for native grass seed set, as explained in the landholder interview. We found that neither *Eucalyptus* nor *Acacia* populations were recruiting and the ground layer at this land-type was heavily invaded by exotic pasture species. Sensitive rangeland grazing may be successful in some areas to improve the health of remnant vegetation, because it removes biomass from competitively dominant groundstorey species (Lunt *et al.* 2007). For instance, in *Themeda* grasslands of the central tablelands of NSW short duration (crash) grazing in autumn resulted in less browsing of *Eucalyptus* seedlings than grazing during spring (Semple and Koen 2001). This suggests the season and intensity of grazing in this Midlands environment may not be most effective for promoting recruitment. Fast rotational grazing could potentially benefit recruitment in areas with scattered trees and an exotic dominated ground layer and can also improve litter cover and water infiltration and increase herbaceous ground cover (Earl and Jones 1996; Sanjari *et al.* 2008; Fischer *et al.* 2009). Trialling different grazing regimes in the grassy woodlands of Tasmania is required. The damaging effects of a rapidly increasing population of feral deer on tree recruitment (Bailey *et al.* 2014; Potts *et al.* 2014) is another topic warranting research.

The senescing trees and recruitment failure in the private conservation and rangelands on Beaufront have been identified in other Australian temperate grassy woodland areas (Saunders *et al.* 1991; Yates and Hobbs 1997). They point to disrupted ecological processes and have been interpreted as imminent ecological collapse (Fischer *et al.* 2009). Elevated macronutrients, soil compaction and grazing or browsing are key causes of woodland degradation (Dorrough *et al.* 2006; Prober and Lunt 2009). With continual livestock grazing and fertiliser use the probability of tree regeneration is low (Fischer *et al.* 2009). Yet removing continuous grazing and fertilisers does not rapidly reverse the trajectory of declining grassy woodland remnants, as shown by the absence of regeneration on the private reserves on Beaufront. Soil fertility takes several decades to return to levels comparable with unfertilised native vegetation (Fischer *et al.* 2009). Even if fertiliser is not

directly applied to remnant vegetation, the effects of stock sheltering near remnants can increase soil nutrients, particularly in small patches (Duncan *et al.* 2008). Methods used to hasten fertility decline include burning, slashing and the addition of carbon, but produce mixed results (Prober and Thiele 2005; Driscoll 2017).

High cover of exotic pasture species and weeds was closely correlated with poor *Eucalyptus* regeneration. Higher cover of exotic grass was found at Beaufront sites than Epping Forest, and was associated with the longer period of European modification at Beaufront. Other studies have also found that high cover of exotic annuals is associated with a lack of native species recruitment (Semple and Koen 2003; Dorrough and Moxham 2005). Exotic pasture species grow densely, and they often possess a thick mat of surface roots that effectively exploit moisture and nutrients, which allows them to survive in compacted soils better than deep rooted perennial species (Skinner *et al.* 2009). Exotic grass species form dense thickets which become moribund over time, and without grazing or other biomass removal they out-compete emerging seedlings for light (Semple and Koen 2003). These species do not leave space in the matrix for other herbaceous species to grow, nor for tree seedlings to germinate (Lunt and Morgan 1999; Semple and Koen 2003). Exotic pasture species grow rapidly, thrive in high nutrient soils and have been selected to be tolerant of trampling. High exotic cover in patches with tree dieback may be associated with high fertiliser use, which both promotes grass growth and adversely affects tree health (Gilfedder and Kirkpatrick 1998). Even in intact forest areas we found evidence of some exotic species invasion. Control of exotic species could therefore assist tree recruitment.

Our study demonstrates important ecological differences between *Eucalyptus* and *Acacia* trees in this highly modified landscape. Old, isolated *Eucalyptus* trees have lower seed production, viability and diminished aerial and soil seedbanks than those occurring in larger patches of remnant vegetation (Burrows 2000). By contrast, *Acacia* seed can remain viable in the soil for many years (Gilbert 1959), so seedlings can emerge in remnant vegetation when grazing is removed. *Acacia*

recruitment was present at all land-types except improved pastures. As a pioneer genus, *Acacia*, is the first to recolonise disturbed or degraded land and helps to improve the soil and provide shelter sites for climax species to grow (Adams and Attiwill 1984; May and Attiwill 2003). *Acacia* species rapidly absorb nutrients from the soil and incorporate them into plant matter. The short lifespan of most *Acacia* species means that nutrients are rapidly returned to the soil in a form available for other plants to use. *Acacia* species thus tolerate anthropogenic disturbance and regenerate more readily than *Eucalyptus* species and their establishment is an important step towards regeneration of degraded patches.

In summary, we show that past land use practices affect the population viability of trees in grassy woodlands reserved for conservation. We acknowledge that land use and vegetation-soil complexes are closely coupled, whereby more productive sites have land use histories that are inimical to tree regeneration. Thus, it is important to consider past land use and current ground layer health and composition if tree species are to persist. To avoid private conservation reserves of grassy woodlands becoming mausoleums, active measures must be undertaken to restore ecological functions and encourage recruitment (Prober and Thiele 2005). Urgent research and restoration efforts should examine how removal of exotic pasture species in private conservation reserves can benefit natural recruitment of overstorey species. Patch burning should be examined to determine appropriate seasonality and frequency to most benefit recruitment of native tree species. Efforts to promote natural regeneration are wasted if overstorey species in private conservation reserves are no longer producing viable seeds: this must be assessed and seed supply supplemented if necessary. Government and non-government conservation agencies need to ensure that landowners are provided with assistance to maintain and improve private reserves. This requires considerable investment and long-term commitment to be successful.

Conflicts of interest

The authors declare no conflicts of interest

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Supplementary materials

Appendix 1. Environmental characteristics of the land-type categories used in this study
Vegetation categories are adapted from TasVeg 3.0. Geology categories are modified from 1: 250,000 Digital Geology Tasmania map, the most common vegetation and geology type for sample points is listed first. Mean values are presented with minimum and maximum values in parentheses. Land-type codes are: B-NF – Beaufront Native Forest: EF-TG – Epping Forest Public Conservation; EF-PC - Epping Forest Private Conservation; B-PC – Beaufront Private Conservation; B-R – Beaufront Rangeland; B-IP – Beaufront Improved Pasture. WB – water balance.

	Land-type	Vegetation category	Geology	Elev. (m)	Slope (degrees)	Rainfall (mm)	WB (mm)
Native Forest	B-NF	*E. viminalis, E. amygdalina*, *E. ovata* woodland and forest, lowland grassland complex	Jurassic dolerite, quartz sandstone, basalt	463 (249–600)	7 (0–20)	600 (513–685)	-173 (-322 – -34)
Conservation	EF-TG	*E. amygdalina* inland forest and woodland on Cainozoic deposits or on dolerite*, E. viminalis* grassy forest and woodland	Cainozoic sediments (Laterite, sands, gravels), Jurassic dolerite	212 (195–238)	2 (0–8)	487 (526–589)	-255 (-313 – -278)
	EF-PC	*E. amygdalina* inland forest and woodland on Cainozoic deposits	Cainozoic sediments (Laterite, sands, gravels)	205 (174–247)			
	B-PC	*E. amygdalina* woodland on dolerite or sandstone, *E. viminalis* woodland, lowland grassland complexes, agricultural land and regenerating agricultural land	Quartz sandstones Jurassic dolerite	260 (233–294)	4 (1–9)	507 (499–517)	-345 (-367 – -310)
Production	B-R	Agricultural land and regenerating agricultural land, *E. viminalis* woodland, *E. amygdalina* woodland on dolerite or sandstone, lowland grassland complexes, *Bursaria-Acacia* scrub	Jurassic dolerite, quaternary sediments, quartz sandstone	267 (213–335)	4 (0–13)	510 (499–534)	-340 (-373 – -293)
	B-IP	Agricultural land, lowland *Poa* grassland, *E. viminalis* grassy forest and woodland, *E. amygdalina* woodland on dolerite	Basalt, Jurassic dolerite, quartz sandstone	217 (196–293)	2 (0–7)	497 (401–511)	-372 (-390 – -338)

Appendix 2. Summary of the statistical models exploring the relationship of tree density in different size classes as a function of land-type

The response variable was the count of trees in each 10-cm DBH class in each transect for each land-type. df shows the number of parameters for each model, ΔAICc the difference between the model AICc and the minimum AICc in the set of models, and AICc weights (w_i) indicate the relative support for model i.

	df	*E. amygdalina*		*E. viminalis*		*A. dealbata*		*B. marginata*	
Model		ΔAICc	wi	ΔAICc	wi	ΔAICc	wi	ΔAICc	wi
SC * land-type	12	0.0	0.969	0.0	1	0.0	1	7.0	0.029
SC + land-type	8	6.9	0.031	44.3	<0.001	49.1	<0.001	0.0	0.971
SC	4	132	<0.001	81.4	<0.001	143	<0.001	21.1	<0.001
Land-type	7	623	<0.001	285.7	<0.001	500	<0.001	74.5	<0.001
Null	3	743	<0.001	326.0	<0.001	584	<0.001	97.8	<0.001

Appendix 3. Density (mean ± s.e.) of live trees by species in five of the six land-type categories.

Improved Pasture land-type is excluded as there were only 13 live *E. viminalis* trees, all at one transect. The number of transects (n) where the species was present is listed. Densities for individual species are averaged for only the plots where the species was present. The species in bold are those used in the statistical analysis. Land-type codes are: B-F – Beaufront Native Forest; EF-TG – Epping Forest Public Conservation; EF-PC – Epping Forest Private Conservation; B-PC – Beaufront Private Conservation; B-R – Beaufront Rangeland; B-IP – Beaufront Improved Pasture. Dashes indicate a species is absent from a land-type category. 'n.a.' indicates not applicable.

Land-type	B-NF			EF-TG			EF-PC			B-PC			B-R		
Species	*n* (transects/ 52)	density (ha^{-1})	s.e.	*n* (transects/ 26)	density (ha^{-1})	s.e.	*n* (transects/ 15)	density (ha^{-1})	s.e.	*n* (transects/ 20)	density (ha^{-1})	s.e.	*n* (transects/ 46)	density (ha^{-1})	s.e.
Acacia dealbata	**35**	**503**	**81**	**21**	**158**	**30**	**15**	**190**	**36**	**3**	**553**	**283**	**9**	**92**	**55**
Acacia mearnsii	6	40	20	3	60	17	-	-	-	2	15	5	8	103	65
Acacia melanoxylon	4	23	6	-	-	-	-	-	-	-	-	-	-	-	-
Acacia – unidentified	1	70	n.a.	2	140	70	-	-	-	-	-	-	-	-	-
Allocasuarina littoralis	2	10	0	10	33	8	4	81	47	-	-	-	2	15	5
Banksia marginata	**2**	**10**	**0**	**14**	**136**	**44**	**7**	**304**	**125**	-	-	-	**2**	**10**	**0**
Bursaria spinosa	9	34	16	1	10	n.a.	-	-	-	1	10	n.a.	-	-	-
Coprosma quadrifida	6	15	3	-	-	-	-	-	-	-	-	-	-	-	-
Eucalyptus amygdalina	**23**	**239**	**52**	**23**	**147**	**16**	**14**	**148**	**24**	**1**	**40**	**n.a.**	-	-	-
Eucalyptus delegatensis	5	228	91	-	-	-	-	-	-	-	-	-	-	-	-
Eucalyptus globulus	1	480	n.a.	-	-	-	-	-	-	-	-	-	-	-	-
Eucalyptus ovata	6	50	32	6	22	5	-	-	-	-	-	-	-	-	-
Eucalyptus pauciflora	4	13	3	-	-	-	3	28	12	-	-	-	1	40	n.a.
Eucalyptus tenuiramis	1	200	n.a.	-	-	-	-	-	-	-	-	-	-	-	-
Eucalyptus viminalis	**36**	**76**	**13**	**14**	**33**	**13**	**14**	**26**	**7**	**9**	**43**	**11**	**8**	**36**	**15**
Eucalyptus - unidentified	2	10	0	3	13	3	1	5	n.a.	-	-	-	-	-	-
Exocarpos cupressiformis	1	10	n.a.	2	25	5	3	8	3	1	10	n.a.	-	-	-
Leptomeria drupacea	-	-	-	-	-	-	1	15	n.a.	-	-	-	-	-	-
Olearia argophylla	1	10	n.a.	-	-	-	-	-	-	-	-	-	-	-	-
Ozothamnus sp.	2	10	0	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 4. Summary of the statistical models exploring the relationship between tree seedling density as a function of land-type for three dominant genera; *Eucalyptus*, *Acacia*, *Banksia*.
The response variable was the count of seedlings in each transect for each land-type. df shows the number of parameters in each model, ΔAICc the difference between the model AICc and the minimum AICc in the set of models, and AICc weights (w_i) indicate the relative support for model i.

		Eucalyptus		*Acacia*		*Banksia*	
	df	ΔAICc	w_i	ΔAICc	w_i	ΔAICc	w_i
Land-type	7	0.0	1	0.0	1	0.0	1
null	2	75.5	<0.001	19.3	<0.001	31.8	<0.001

Appendix 5. Density and standard error (s.e.) by species of seedlings in five of the six land-type categories

No seedlings were found at the Improved Pasture land-type. As for Appendix 3 except for seedlings. Only live seedlings were recorded. Land-type codes are: B-F – Beaufront Native Forest; EF-TG– Epping Forest Public Conservation; EF-PC – Epping Forest Private Conservation; B-PC – Beaufront Private Conservation; B-R –Beaufront Rangeland. 'n.a.' indicates not applicable.

Land-type	B-NF			EF-TG			EF-PC			B-PC			B-R		
Species	*n* (plots/ 52)	density (ha^{-1})	s.e.	*n* (plots/ 26)	density (ha^{-1})	s.e.	*n* (plots/ 15)	density (ha^{-1})	s.e.	*n* (plots/ 20)	density (ha^{-1})	s.e.	*n* (plots/ 46)	density (ha^{-1})	s.e.
Acacia dealbata	**22**	**2036**	**572**	**16**	**713**	**202**	**13**	**415**	**72**	**3**	**1666**	**796**	**4**	**3624**	**1888**
Acacia mearnsii	2	100	0	2	250	150	-	-	-	-	-	-	2	150	0
Acacia melanoxylon	1	200	n.a.	1	11700	n.a.	-	-	-	-	-	-	-	-	-
Acacia - unidentified	5	2780	1928	2	300	282	-	-	-	-	-	-	1	1000	n.a.
Allocasuarina littoralis	-	-	-	3	67	17	1	325	n.a.	-	-	-	1	200	n.a.
Banksia marginata	**3**	**233**	**33**	**12**	**371**	**220**	**6**	**1013**	**455**	**-**	**-**	**-**	**2**	**50**	**0**
Bursaria spinosa	8	238	74	1	100	n.a.	-	-	-	1	100	n.a.	1	50	n.a.
Coprosma quadrifida	8	625	273	-	-	-	-	-	-	-	-	-	-	-	-
Eucalyptus amygdalina	**11**	**614**	**228**	**19**	**432**	**100**	**13**	**192**	**51**	**-**	**-**	**-**	**-**	**-**	**-**
Eucalyptus delegatensis	4	313	263	-	-	-	-	-	-	-	-	-	-	-	-
Eucalyptus ovata	2	1175	1125	6	233	68	-	-	-	-	-	-	-	-	-
Eucalyptus pauciflora	2	50	0	-	-	-	-	-	-	-	-	-	1	200	n.a.
Eucalyptus tenuramis	1	200	n.a.	-	-	-	-	-	-	-	-	-	-	-	-
Eucalyptus viminalis	**15**	**93**	**19**	**2**	**50**	**0**	**6**	**29**	**4**	**1**	**50**	**n.a.**	**1**	**150**	**n.a.**
Eucalyptus – unidentified	2	125	25	1	350	n.a.	-	-	-	-	-	-	-	-	-
Exocarpos cupressiformis	-	-	-	1	250	n.a.	-	-	-	-	-	-	-	-	-
Lomatia	1	1150	n.a.	-	-	-	-	-	-	-	-	-	-	-	-
Lycium ferocissimum	-	-	-	-	-	-	-	-	-	1	150	n.a	-	-	-
Ozothamnus	1	1800	n.a.	-	-	-	-	-	-	-	-	-	-	-	-
All acacias	28	1137	331	20	931	452	13	360	72	3	250	169	6	350	36
All eucalypts	28	247	74	20	386	87	13	177	49	1	3	2.5	2	8	5
All species	38	1018	34	21	1019	59	15	750	56	4	140	19	7	190	16

Appendix 6. Summary of the statistical models exploring the relationship between tree sapling density as a function of land-type for three dominant genera; *Eucalyptus*, *Acacia*, *Banksia*.
The response variable was the count of saplings in each transect for each land-type. df shows the number of parameters in each model, ΔAICc the difference between the model AICc and the minimum AICc in the set of models, and AICc weights (w_i) indicate the relative support for model i.

		Eucalyptus		*Acacia*		*Banksia*	
	df	ΔAICc	w_i	ΔAICc	w_i	ΔAICc	w_i
Land-type	7	0.0	1	0.0	1	0.0	1
null	2	72.5	<0.001	23.1	<0.001	30.5	<0.001

Chapter 4 Synthesis

No going back: The irrevocable transformation of Tasmania's grassy woodlands since European settlement

The changing natural values of Tasmania's woodlands

Around the globe, a band of comparable vegetation found at ~40° north and south of the equator has been a focal region for human activity for millennia (Murphy and Ehrlich 1989; Baldocchi *et al.* 2004; Olea and San Miguel-Ayanz 2006). Open temperate grassy woodlands and savannas have been the preferred habitat for humans in Europe, North and South America, Asia, Africa and Australia for so long that the preference now appears inherent (Falk and Balling 2010). In temperate grassy woodlands, trees are widely spaced or form small copses and punctuate a productive, grassy and herbaceous ground layer. Temperate grassy woodlands and savannas provide food resources and attract prey for hunting. Globally, humans often feel comfortable in woodlands because the field of view is expansive, safety can be appraised and prey can be found easily (Falk and Balling 2010). These qualities are captured in Appleton's (1975) prospect and refuge theory which encapsulates both the opportunity (prospect) and safety (refuge) offered by sparsely treed landscapes. Tasmania's temperate grasslands and temperate grassy woodlands form the southernmost extension of the global distribution of temperate grassy woodlands. These areas are important for agricultural production and settlement. Within this landscape, native biodiversity plays an important role in enabling continuation of an environment that is hospitable to human use. Policy makers face the challenge of sustainably managing these biomes in the face of apparently incompatible pressures of agriculture and settlement. Throughout this chapter I refer to this complex of temperate woodland landscapes as 'temperate grassy woodlands' to clearly distinguish them from tropical savanna.

In this thesis I have examined the Midlands of Tasmania as a microcosm of temperate grassy woodlands worldwide. The anthropogenic changes generated, first by Aboriginal, then European people in the Tasmanian Midlands have accelerated with the technological development of its inhabitants. Climate change is likely to cause a further acceleration of these changes making the region less suitable for existing native vegetation and for current forms of agricultural production and human occupation more generally. In this chapter I trace the history of human interaction with this landscape, from the original Aboriginal inhabitants to the first European yeoman farmers through to the current industrial agricultural landscape. The Tasmanian Midlands is an ideal case study of the interplay between biodiversity and human needs. In

the current landscape, the tension between biodiversity conservation and agricultural productivity within a privately-owned region continues to evolve.

This thesis set out examine the following aspects of landscape change in the Tasmanian temperate grassy woodlands

Chapter 1

By examining sediment cores from the Tasmanian Midlands, I identified

1.1 Changes in vegetation patterns after the arrival of European settlers.

1.2 Increased use of fire in the Midlands after the arrival of European settlers.

1.3 Minimal evidence of Aboriginal fire use prior to European settlement and hints at aboriginal food sources being present in the landscape.

Chapter 2

I used analysis of remotely sensed data for the Tasmanian Midlands to document

2.1 An increase in landscape clearing during 1945-2010 compared to 1788-1945.

2.2 7.2Mt of carbon was lost from the landscape since Europeans arrived through land clearance for agriculture.

2.3 The extent of revegetation required to replace the carbon lost through vegetation clearance for agriculture and mitigate the projected effects of climate change would not be feasible in a productive landscape.

Chapter 3

I used demographic analysis of replicated vegetation plots to determine that

3.1 public and private reserves differ in their effectiveness in protecting the survival and recruitment of overstorey tree species which was largely dependent on land use history.

3.2 Private conservation reserves were not effective in preserving overstorey tree species and promote recruitment.

3.3 Prior land use history influences success of reserves in protecting survival and recruitment of overstorey tree species.

What follows is an account of the evolution of two distinct cultural landscapes, Aboriginal and European, from the Pleistocene to the present that highlights where this study contributes to our understanding of the past and likely future of the temperate grassy woodlands of the Tasmanian Midlands.

People, climate and fire - An Aboriginal cultural landscape

Tasmania during the last glacial period was harsh but habitable and supported a resilient human population who successfully exploited the landscape to meet their needs. Until 43,000 – 35,000 years ago, Tasmania, Australia's southernmost island, was unoccupied and unaffected by human activity (Cosgrove *et al.* 1996; O'Connell and Allen 1998). When Aboriginal people migrated to Tasmania, the Bassian land bridge linked mainland Australia and the present island of Tasmania (Lambeck and Chappell 2001). At that time Tasmania was glaciated and colder, drier and less seasonal than today (Lewis 1945; Pyne 1991; Colhoun and Shimeld 2012). The varied geology and mountainous topography created a range of habitats which provided seasonally suitable shelter and vegetable resources for the first human occupants. The coastline was resource rich and longer than it is today because sea levels were 60 – 120 m lower than present (Colhoun and Shimeld 2012). It is difficult to imagine the cold, glacier-covered island as habitable for these first human settlers, but archaeological evidence indicates that food and shelter resources were adequate and hunting productive (Pike-Tay *et al.* 2008).

Tasmania has undergone several climactic shifts since first human occupation, which have caused alterations to the vegetation of the island. While a detailed picture of vegetation change has been reconstructed for western and north western Tasmania, the east is less well understood. Several well-preserved sediment cores have been extracted from permanent waterbodies on the north and western half of the island with pollen and fossilised vegetation from these cores used to reconstruct patterns of vegetation change (Colhoun and Shimeld 2012). A paucity of permanent waterbodies in the dry, eastern side of the island has made climate reconstruction more challenging. The notable exceptions in the east are long sediment records from Crown, Hazards and Stoney Lagoons (Sigleo and Colhoun 1981; Jones *et al.* 2017; Mackenzie and Moss 2017). Sediment records from north east Tasmania document changes from

cold grassland to grassy woodland to *Allocasuarina* dominated heathland (Thomas and Kirkpatrick 1996). Sediment cores from Crown Lagoon suggest that, like the north west, the east was also cold and dry during the last glacial maximum (LGM) (22,000–18,000 cal BP). The vegetation changed from savanna with *Eucalyptus* and *Allocasuarina* to open grassland with very few trees and a high proportion of Poaceae, Asteraceae and Chenopodaceae throughout the last glacial period (Sigleo and Colhoun 1981; Jones *et al.* 2017; Mackenzie and Moss 2017). Low concentrations of charcoal in sediment records throughout the LGM suggest there was insufficient biomass to support large landscape fires (Mackenzie and Moss 2017).

Fire is an important cultural tool that Aboriginal people have used to manipulate the landscape for millennia with the practice termed 'fire stick farming' (Jones 1969; Bliege Bird *et al.* 2008). The sediment record suggests that most fire in Tasmania is likely to have been the result of human sources of ignition since natural sources of ignition (i.e. fire caused by lightning strikes) were rare (Bowman and Brown 1986; Pyne 1991). Burning grasses encouraged green growth which attracted prey. Fire was also used to flush prey from cover (Jackson 1999). Burning was the main cultural tool used for hunting red-necked Wallaby (*Macropus rufogriseus*) (Cosgrove 1999; Fletcher and Thomas 2010).

The Pleistocene environment of the eastern side of Tasmania was challenging for human occupation because precipitation was unpredictable and resources highly variable across the landscape (Cosgrove *et al.* 1990). Palaeological evidence suggests that during the LGM a cold, dry climate in conjunction with Aboriginal burning caused massive erosion (Sigleo and Colhoun 1982). Aeolian activity created a series of dune and lunette systems during the period between 29,000 cal BP and 14,500 cal BP (Sigleo and Colhoun 1982). In the cold and dry climate, grass growth would have been impaired meaning the use of fire at unsuitable return intervals may have contributed to a near total loss of ground cover. Fire regimes suited to different climatic zones such as mainland Australia, may therefore not have been appropriate for glacial Tasmania, and Pleistocene era Tasmanians may not have been always able to match appropriate fire use with changing climate (Sigleo and Colhoun 1982). This implies that vegetation was heavily influenced by both climate and people during this period (Colhoun and Shimeld 2012).

As temperatures rose during the end of the Pleistocene and beginning of the Holocene (around 12,000 BP), vegetation structure changed throughout the Midlands. During this period, trees invaded open grasslands and vegetation began to shift towards a more savanna- or woodland-like formation. Pollen of *Eucalyptus*, *Pomaderris* and *Phylocladus* species increased in abundance in sediment records from this period (Jones 2008) and species composition was similar to modern grassland or temperate grassy woodland assemblages (Jones *et al.* 2017). The open grassy environments that existed during this period would have provided good food resources for herbivores, so it is reasonable to expect that Aboriginal people hunted in the region but conclusive evidence of this is scarce. Jones *et al*. (2017) found little palynological evidence of landscape scale fire in these grassy environments at the end of the Pleistocene. While fire is integral to the maintenance of some grassland and woodland landscapes (Bowman *et al.* 2013), little evidence has been found that these grassy systems were more influenced by fire than climate.

Early researchers believed that eastern Tasmania was burnt regularly by Aboriginal people at the time of European arrival, a supposition based on early explorer accounts (Thomas 1991). Yet, the importance of fire in shaping the temperate grassy woodlands of Tasmania is not elucidated in palynological records from the latter part of the Holocene. In the early Holocene the climate dried and rainfall events became more variable, with a concurrent increase in regional fire activity (Jones *et al.* 2017). However, throughout the Holocene evidence of regional scale fire decreased (Jones *et al.* 2017).

In this study (Chapter 1), small amounts of macroscopic charcoal were found in sediment records from the period 400 years prior to European arrival in the Midlands. I examined a network of ephemeral lagoons throughout the region and found evidence suggestive of local, low intensity and patchy burning (Chapter 1.3, supplementary material). However, whether the source of this burning is anthropogenic or not, cannot explained by this evidence and further investigation is warranted.

The debate about whether Australian grasslands and temperate grassy woodlands are a cultural landscape or driven by abiotic factors remains unresolved. The open and park-like environment that the first Europeans found when they settled Tasmania has been attributed to Aboriginal burning (Jackson 1968; Pyne 1991; Gammage 2011). Gamage (2008) posits that without Aboriginal burning there would have been

much more rainforest in Tasmania and that Aboriginal fire created grassland and open temperate grassy woodland. Throughout the Holocene, palynological records show a shift away from grassy understorey communities to shrubby communities typical of dry sclerophyll forest in the east of Tasmania (Sigleo and Colhoun 1981; Jones *et al.* 2017).

No long-term record for the lowland areas of the Midlands is available. However, I found evidence (Chapter 1.3) from the latter part of the Holocene, immediately prior to European arrival, of a grassy eucalypt and *Allocasuarina* dominated landscape through the lowland areas of the Midlands. In sediment records from other parts of Tasmania the transition away from grassy understoreys has been attributed to declining soil fertility in combination with a warming climate, increasing fire and the salt laden winds blowing from a newly stabilising coastline (Thomas and Hope 1994; Thomas and Kirkpatrick 1996). Additional factors such as soil moisture, soil pH and fire have also been attributed to the patterning of vegetation in the Midlands (Fensham 1989). Mounting evidence from various sources, suggests that these ecosystems, at least in the eastern half of Tasmania, were driven by climate, geography, soils and moisture availability (Fensham 1989) and were merely modified by Aboriginal use (Chapter 2)(Macphail and Jackson 1978; Thomas and Kirkpatrick 1996).

Evidence that Aboriginal use of fire was important in forming vegetation complexes exists for other areas of Tasmania and for other geological periods (Fletcher and Thomas 2010a; Fletcher and Thomas 2010b; Bowman *et al.* 2013) but it is lacking for the period just prior to European arrival in the Midlands of Tasmania. The absence of evidence of Aboriginal fire in this area does not rule out the possibility that it was used and that it impacted on the vegetation composition of these woodlands. However, my findings suggest that Aboriginal land management perhaps did not create the open woodland landscape of the Midlands, rather, Aboriginal people used existing environmental characteristics useful for survival which included plant and animal food sources, tree cover for material resources, refuge and habitat for game.

Clearance and land use change – creation of a European agricultural landscape

> *'We came with visions but not with sight. We came with visions of former places but not the sight to see where we were.'* (The Unsettling of America, Berry 1977)

In Europe during the late 18th century, the rapid growth of human populations following the industrial revolution, competition for resources and advances in transport and navigation led Europeans to expand their empires to new continents, creating a trail of 'neo-Europes' in their wake (Crosby 1986). Australia was colonised by Britain with the first white settlers arriving in Tasmania in 1803. The Midlands of Tasmania was favoured by the first English settlers for its open landscapes with rolling hills and luxuriant grasslands and a climate which more closely resembled England's than did that of New South Wales (Morgan 1992). Widely spaced trees and native perennial grasses meant the land running north-south between Tasmania's two major estuaries, the Derwent and the Tamar with their port cities of Hobart and Launceston, was easily converted to pastoral land with minimal clearance (Smith 1960; Lines 1991; Jackson 1999). By the mid-1830s over 2 million acres had been granted or sold throughout Tasmania and most of the grasslands and temperate grassy woodlands in the Midlands and east coast had been settled (Easteal 1971). Within 25 years of European arrival, the landscape was largely transformed from Aboriginal management to neo-European farms.

Like the previous custodians of the land, the new European landowners managed the land to conform to their own suite of preferred traits both aesthetic and functional. The British brought with them cultural traditions regarding weather, land use and property (Evans 2012) and it was psychologically easier for the new settlers to manipulate the landscape to match these traditions rather than change their internal traditions to match the land. The English colonists planted species that reminded them of home, many for sentimental rather than economic reasons (Robin *et al.* 2011).

Even at the time of Federation in 1901, Australians still called themselves 'British Australians' (Robin *et al.* 2011). In many ways, this English cultural influence still exists in the Midlands. The grand manor houses, large gentlemen's estates, delimited by hedges of hawthorn trees with sheep grazing the hillsides and willow fringing the banks of rivers and streams lend an air of England to this otherwise very Australian landscape. During winter and spring, and longer in wet years, the landscape is green and lush. During summer the similarity to England dissolves, the burnt yellow grasses and skeletons of dead eucalypts give the landscape a quintessentially Australian appearance. While cultural traditions and attitudes towards

Tasmania have been modified over the years by a harsher climate and isolation from the 'motherland', a British essence remains.

Fire was also instrumental in creating a new, European-influenced, Midlands landscape. The arrival of Europeans in Australia is marked in the palaeological record by a sharp increase in macroscopic charcoal (Mooney *et al.* 2001; Black and Mooney 2006). Consistent with this, my study (Chapter 1.2) identified a marked increase of macroscopic charcoal in the Tasmanian Midlands over the last 200 years, signifying a greater frequency of local fires soon after European settlement (Romanin *et al.* 2016). As mechanical means of clearing the land were limited, European settlers used fire liberally to create the landscape they favoured. Fire was an easily adopted tool to manipulate the landscape and was particularly useful for removing acacias (Gilfedder *et al.* 2003).

Fire was also used to encourage green pick for stock until the 1960s, with some landowners believing they were continuing the fire use practices that they had learned from Aboriginal people who had been burning in Tasmania for 40,000 years (Kirkpatrick 2007a). However, it is likely that European burning was much larger in scale and much less sensitive to climactic conditions, season and vegetation than that of contemporary Aboriginals. Additionally, in the fight for possession of Tasmanian land, both sides, British and Aboriginal, weaponised fire (Pyne 1991; Thomas 1994; Boyce 2008). Further evidence of land use change in the transition from Aboriginal to European management has also been found in palaeological and tree ring studies (Jones 2008; von Platen *et al.* 2011; Jones *et al.* 2017). Perhaps the strongest lesson we can infer from the increase in fire recorded in the Midlands is that it was markedly different to the record left by Aborigines.

The appearance of exotic species in the palynological record provides another clear indicator of a transition to European land management (Romanin *et al.* 2016). Indicator species are used in ecological studies to signal changes to environmental conditions, and some exotic genera are so linked with European settlement that they are used as indicators which signal the presence of a group of people in a new land. In this study (Chapter 1.1), *Pinus* was used to clearly separate pre- and post-European periods. The first appearance of *Pinus* type pollen determined by carbon dating closely corresponded to European

occupation. Some exotic plant species are visible in the palaeological record and have left their mark on the landscape from the early 19th century to the present (Romanin *et al.* 2016).

Exotic grass species, on the other hand, cannot be clearly separated from native grasses based on pollen morphology. However, we know that many pasture species arrived with early settlers and stock and spread rapidly (Lines 1991). Tasmanian grasslands and temperate grassy woodlands were quickly colonised by species such as perennial ryegrass (*Lolium perene*), cocksfoot (*Dactylis glomerata*) and white clover (*Trifolium repens*). The climate of Tasmania was particularly suitable for these and many other temperate species and some species such as gorse (*Ulex europaeus*) have become overabundant and troublesome (Lines 1991).

Evidence of land clearance, overstocking and erosion can be read in the sediment record from increased rates of deposition. Grazing by sheep and other hard hooved species modify native grasslands and enable annual and perennial exotic grasses and forbs to invade (McIntyre and Lavorel 1994a). Undisturbed grasslands remain resistant to invasion by exotics but close and regular grazing by livestock or feral animals such as rabbits plus trampling alters species composition. Many native species are sensitive to livestock disturbance and are replaced by rapidly growing exotic annuals which are pre-adapted to major disturbances (McIntyre and Lavorel 1994b). Livestock grazing selects for short statured native forbs and exotic rosette species which alters the structure of grasslands (Bridle and Kirkpatrick 1999).

Exotic species are often less resilient to drought and leave paddocks bare after even a short period of hot spring weather (Lines 1991). As degraded pastures lose deep rooted perennial grasses, they become vulnerable to erosion. In the period soon after European settlement, rapid erosion occurred in Southern Midlands, with more sedimentation attributable to two centuries of European occupation than the previous two millennia of Aboriginal habitation (Sigleo and Colhoun 1982). However, in this study (Chapter 1) no evidence of an increase in sedimentation rate was found. This data was extracted from an ephemeral lagoon in the north of the Midlands, close to Epping Forest. As discussed later in this chapter, land clearance occurred later here than in the rest of the Midlands and local grazing may have been less intense thus causing lower levels of erosion in this area.

Efforts to intensify agricultural production began in the 1840's utilising tree clearing primarily in temperate grassy woodlands to increase the area available for cultivation (Romanin *et al.* 2015). Areas of fertile grassland and temperate grassy woodlands in the Midlands are limited by topographic position with the lowlands bracketed on the east and west by forested hills which mark the boundaries of an ancient graben (Easteal 1971). In the early period of settlement, technology limited the rate of land clearance and ringbarking was the most efficient method of tree removal. Ringbarked trees were burned, and grass seed was broadcast into the ashes (Easteal 1971). Fallen timber was left in paddocks for stock to graze around.

Early farming enterprises used convict labour but, after transportation ceased in 1853, labour shortages developed, and farmers were forced to become more efficient. The 1870s and 1880s marked the beginning of a transition to mechanised farming (Easteal 1971). Ploughs became cheaper, stronger and lighter in the 1870s, enabling more efficient conversion of grasslands to cropland, but they were only effective on relatively flat ground cleared of stones. Alluvial soils were preferred by the first settlers because they remained productive under repeated cropping. This preference for fertile soils means that native vegetation is virtually extinct in these areas (Kirkpatrick 1991; Gilfedder and Kirkpatrick 1994). But even in these productive areas eventually soil fertility declined and had to be supplemented artificially. Fertilisers were first imported into Tasmania during this period, with guano used for cereal crops (Easteal 1971).

The early attempts to rectify declining soil fertility were ineffective and by the 1920s agricultural productivity of the Midlands had deteriorated due to a century of unsustainable farming practice (Kellaway 1989). During the late 1920s the Tasmanian government sought to ameliorate soil fertility by advocating a shift in farming practice away from cropping in favour of intensive livestock farming (Kellaway 1989). It was believed that inputs in the form of animal manure would rectify fertility problems. At the same time there was thickening of forest vegetation in the low hills surrounding the Midlands in response to disturbance, with sapling growth reducing the area of available land for agricultural enterprises (Kellaway 1989). It was not until the late 1930s that artificial fertilisers had become affordable enough to really benefit the productivity of farms (Kellaway 1989).

The rapid loss of tree cover post 1940s, when mechanised clearing became widely available, resulted in an increase in agricultural production. In this study (Chapter 2.1) I estimate that the rate of clearing during the period 1945-2010 was approximately three times greater than that occurring between 1788 and 1945 (Romanin *et al.* 2015). After the 1940s nitrogen and superphosphate fertilisers were applied, machinery for tilling the soil became more widely used, more diverse crop species were planted and yields increased (Gilfedder *et al.* 2003). With improvements in rectifying soil deficiencies it now became viable to clear marginal soils for agriculture. For example, Epping Forest is found on nutrient poor, weathered laterite soils and was not cleared until much later than the rest of the region since trees were denser and the land considered less suitable for agriculture. The first aerial photos were taken at this time, objectively recording the vegetation that existed at the cusp of modern agriculture.

I identified a dramatic reduction in tree cover throughout the entire region by comparing 1940s aerial photography with current satellite images. During the 1980s large areas of native vegetation were cleared. Sclerophyll forest, temperate grassy woodlands and inland grassy forests were cleared at their highest rate during this period (Kirkpatrick 1991), with a large increase in clearance from the 1940s to the 1990s (Fensham and Kirkpatrick 1989). The accelerated rate of clearing created more productive land for agriculture and in the process released an estimated 1.24 Mt of stored carbon into the atmosphere which resulted in a decrease in carbon storage of 21% since 1940s (Chapter 2.2). The carbon stored in the Midlands landscape now is approximately 32% lower than when Europeans arrived in Tasmania. Globally, the area of land cleared for agriculture began to slow from the 1950s as the amount of arable land became scarce (Steffen *et al.* 2015). However, in a 'new' country like Australia, land clearing was accelerating.

The Midlands landscape today

Vegetation in the Midlands is now a mosaic of temperate grassy woodlands, grasslands, derived grasslands, semi native grasslands with a substantial component of exotic pasture species and arable agricultural land. Because productive land is so extensive, areas of native vegetation are limited. Two lowland grassland complexes are critically endangered and protected by federal legislation (Department of the Environment Water Heritage and the Arts 2009). Temperate grassy woodlands, on the other hand, are unlisted and

remain vulnerable to extinction or radical transformation. The Midlands bioregion is classified as one of 15 national biodiversity hotspots in Australia (Department of the Environment and Energy 2014) acknowledging the richness of unique plant and animal species that are threatened by degradation and vegetation loss through clearing, salinity, weeds and vertebrate pests (Myers *et al.* 2000).

Figure 1. A typical scene in the Tasmanian Midlands showing premature dieback of Eucalyptus trees which, coupled with a lack of recruitment, has led to a loss of temperate grassy woodland.

In many areas of remnant temperate grassy woodlands, premature death of the dominant *Eucalyptus* trees is widespread (Figure 1). This phenomenon, known variously as 'rural tree decline' or 'rural dieback', has been attributed to several factors closely linked with agriculture (Neyland 1999). Throughout the Midlands tree decline is particularly noticeable in the driest areas (Neyland 1999). Isolated trees in recently modified landscapes such as this have been identified as keystone structures (Manning *et al.* 2006). These isolated trees are disproportionately important in the environment and are highly valued by graziers (Sherren *et al.* 2011). The loss of trees from the landscape affects ecosystem functions including water infiltration, prevention of dryland salinity, provision of habitat for birds and insects and soil nutrient enrichment (Eldridge and Freudenberger 2005; Manning *et al.* 2006). The loss of large trees from the environment has far reaching impacts on the landscape.

Over 90% of the land area of the Midlands is privately owned, and the average size of farms within the Midlands is 1750 ha, more than four times larger than the average found in the rest of the state (Gadsby *et al.* 2013), a legacy of the colonial administration in the 19th century which consciously attempted to replicate the landscapes of rural Britain through the allocation of large estates to those with capital and

smaller grants near regional centres to other free settlers and convicts (Robson and Roe 1985). Within this largely privately-owned area, between only 1% (Males 2009; Cowell *et al.* 2013) and 8% (Lefroy 2011) of the region is publicly reserved for conservation.

Various schemes have been instigated to encourage conservation on private land, thereby supplementing the public conservation system. However, the capacity of the state government to bear the costs of conserving native grasslands and temperate grassy woodlands is limited because as well as the above average property size, there are high levels of socio-economic disadvantage in the Tasmanian Midlands, with low levels of employment, low average income and limited access to quality education (Gadsby *et al.* 2013; ABS 2018). Thus, the goodwill of landowners is paramount in conserving the natural values of their properties through private conservation reserves. The complexities of creating and maintaining effective conservation programs within the Midlands has been the subject of research for nearly 40 years (Kirkpatrick and Glasby 1981). The conflicts and trade-offs of preserving nature in productive landscapes is emerging as one of the complex issues facing land owners, land managers and conservation scientists worldwide (Fischer *et al.* 2014; Laurance *et al.* 2014; Raymond *et al.* 2015).

The largest public conservation reserve in the northern part of the Midlands, the Tom Gibson Nature reserve, is a 1020 ha remnant of Epping Forest, a *Eucalyptus amygdalina* forest on Cainozoic deposits. Epping Forest is not representative of most of the original vegetation of the Midlands. Early Europeans noted a distinct boundary between Epping Forest and the surrounding vegetation and were struck by the contrast between 'bush' and open plain (Fensham 1989). The former extent of Epping Forest has been reduced and fragmented but numerous small patches of forest remain, most on private property (Fensham and Kirkpatrick 1989; Kirkpatrick 2007a). Tom Gibson reserve was declared in 1991 and today it supports diverse, healthy vegetation with demographically secure tree populations (Chapter 3) within an otherwise heavily fragmented landscape (Figure 2). The remains of Epping Forest are protected through numerous small conservation covenants on private properties.

Figure 2. Fragmentation of Epping Forest in the Northern Midlands of Tasmania between a) 1940s and b) 2010. Small patches of native vegetation remain, especially at roadsides.

In contrast to the Epping Forest area, remnants of native vegetation on fertile lowland valleys near rivers, including grassland and temperate grassy woodland, are very limited, highly fragmented and poorly reserved. Only small areas of the former extent of temperate grassy woodland and lowland grassland still exist (Kirkpatrick *et al.* 1995; Department of the Environment Water Heritage and the Arts 2009). Throughout the Midlands very little native vegetation with a significant grassy component is publicly reserved, the only public grassland reserve being a 16 ha patch of native lowland grassland at Township Lagoon near the town of Tunbridge which provides habitat for 114 native species, 16 of which are endangered, vulnerable or rare (Zacharek *et al.* 1997).

Lowland native grasslands in the Midlands are listed as critically endangered under the *Environment Protection and Biodiversity Conservation (EPBC) Act 1999*, the Australian Government's environmental legislation (Gadsby *et al.* 2013). There are two major sub-types of grasslands which are characterised by the dominant perennial grass species: lowland *Poa labillardierei* grassland and lowland *Themeda triandra* grassland. *P. labillardierei* type grasslands are species poor, whereas *T. triandra* grasslands typically have

high species diversity, including wildflowers and orchids, within the inter-tussock spaces (Kirkpatrick *et al.* 1988; Gilfedder *et al.* 2003; Harris and Kitchener 2016). However, without adequate management *T. triandra* can become dominant and exclude other species (Fensham and Kirkpatrick 1989). Lowland native grassland is highly fragmented and most patches (approximately 80%) are under 10 ha in size (Threatened Species Scientific Committee 2006), most of these occur on 10 – 12 properties (Clement *et al.* 2017). Many of the conservation reserves on private land throughout the Midlands have been created to preserve lowland grassland. Lowland grasslands require ≤10% *Eucalyptus* cover, meaning no conservation effort is invested in encouraging overstorey recruitment in these areas.

The remnants of temperate grassy woodlands which exist in a matrix with lowland grasslands throughout the Midlands are not federally listed for conservation in any way, despite having understoreys very similar to lowland native grassland. This study found that small private temperate grassy woodland reserves in the agricultural matrix often have no overstorey recruitment (Chapter 2.2). Since many reserves on private land serve their stated purpose of preserving endangered grasslands, a lack of *Eucalyptus* recruitment is not regarded as important for that target. In fact, *Eucalyptus* recruitment would contradict grassland structural guidelines in most cases.

These reserves may not be sufficient to preserve temperate grassy woodland communities in the long term and few incentives are in place to protect temperate grassy woodland remnants. But this neglects the ecological importance of scattered trees, including paddock trees, in the landscape (Manning *et al.* 2006) and disregards the decline of *E. ovata* and *E. amygdalina* woodland communities which are threatened at the state level (Department of Primary Industries Parks Water and Environment 2015). The cover of exotic species and increased soil fertility in agricultural land, including within small private reserves, is closely correlated to, and likely implicated in, a lack of eucalypt recruitment (Chapter 2.2). This suggests that active management strategies are needed to reverse this trend and promote recruitment.

What can be inferred about the future of Tasmanian woodlands?

The Midlands has been modified so far from its historical state that the landscape would now be nearly unrecognisable to its first inhabitants. Vast areas of trees have been cleared (Romanin *et al.* 2015), exotic

plant and animal species have been introduced (Romanin *et al.* 2016), eucalypts in grassy woodlands fail to reproduce (Chapter 3), and the region continues to be transformed by irrigated agriculture and by a warming climate. In this situation of massive and ongoing change, it is pertinent to examine the drivers of the future landscape.

This study (Chapter 2.2) estimated that 4.8 Mt of carbon has been lost from the Midlands since European arrival through the clearing of woodlands (Romanin *et al.* 2015). To mitigate the effects of climate change, policy makers have advocated sequestering carbon in soil and vegetation (Garnaut 2011). It is estimated that carbon biomass accumulation in restoration plantings could take between 50 and 100 years to resemble the carbon content of remnant forests (Prior *et al.* 2015) and would require large areas to be dedicated towards plantations (Romanin *et al.* 2015).

This study estimated (Chapter 2.3) that 17,842 ha would need to be revegetated to replace the stored carbon lost through clearing of woodlands that has occurred since European settlement. In a landscape that has been so transformed and which continues to be a dominated by agriculture, it is highly unlikely that it will be possible to balance both carbon sequestration and the financial demands of a productive landscape unless there is a significant increase in demand for the commercial products of woody species that can be grown in relatively short rotations. For these reasons, using an agricultural landscape for carbon capture is unlikely to be successful or adopted by landowners. For example, one current revegetation strategy is the creation of wildlife corridors to increase connectivity within the Midlands landscape and hence the viability of isolated populations of native fauna (Lechner *et al.* 2015). However, at most these will occupy 6 –10,000 ha when complete (Bailey *et al.* 2014; Greening Australia 2018) which will fall short of replacing the carbon debt.

Replacing and storing carbon as vegetation biomass may be impractical but some land use practices can encourage soil carbon stores (Young *et al.* 2005). Perennial pasture systems store much more carbon in the soil than annual systems; the soil carbon storage of improved pastures is similar to unploughed woodland soils after 15 years of establishment (Young *et al.* 2005). In a productive landscape such as the Midlands,

shifts towards productive perennial crops could go some way to increasing carbon storage without sacrificing profit or productive land.

This study (Chapter 3.2) found that private conservation reserves were not effective in preserving demographically sound populations of overstorey *Eucalyptus* species, despite some having been fenced from stock for up to 30 years. This indicates that ecological barriers exist which prevent successful *Eucalyptus* recruitment. Successful recruitment of *Eucalyptus* often requires a rare combination of large-scale disturbance such as fire or flood with germination followed by above-average rainfall (Burrows *et al.* 1990; Yates *et al.* 1994). Natural *Eucalyptus* regeneration is inhibited by multiple factors including competition from exotic plant species (Lawrence *et al.* 1998; Skinner *et al.* 2009), increased soil fertility (Duncan *et al.* 2008), soil compaction (Skinner *et al.* 2009), disruption of long established disturbance regimes including fire (Vesk and Dorrough 2006) and climate change effects including drought (Semple and Koen 2003). The further a remnant and the matrix it inhabits have moved from the undisturbed state, the more challenging it is to force a transition back across a restoration threshold towards its original state (Chapter 3.3; Hobbs *et al.* 2014).

Invasion by exotic species in combination with accelerating climate change may cause significant disturbance to temperate grassy woodland remnants. Climate change is likely to hasten invasion of exotic grasses because many exotic pasture species use the C_4 photosynthetic pathway, meaning they have greater water use efficiency, greater drought tolerance and are better able to tolerate high temperatures (Pau *et al.* 2013). C_4 grasses are likely to promote more frequent and intense fires given their high summer biomass accumulation (D'Antonio and Vitousek 1992; Harris *et al.* 2016). Methodologies have been developed to identify putative problematic invasive taxa under future climates which could be used to prioritise weed management efforts in the Midlands (Gosper *et al*. 2015). Cumulative changes to the composition and structure of remnant vegetation are likely to also cause a shift to an undesired stable state from which return will be extremely difficult or impossible (Harris *et al.* 2016).

After 200 years of agricultural disturbance, ecological thresholds have been crossed in the remnants of native vegetation. It is unlikely that the historical vegetation state of the Midlands landscape can be

recovered without significant investment of time and energy (Westoby *et al.* 1989; Yates and Hobbs 1997b). Nonetheless, each individual remnant is likely to have been pushed into a different state, thus preserving a different subset of the original biota or ecosystem service (Lunt and Spooner 2005). The particular set of land use histories that a remnant has been exposed to will select for and preserve separate elements of the original landscape, such as groundstorey taxa, pools of genetic diversity, or old, hollow bearing trees which provide habitat for fauna. It is important to conserve and link remnants in varied states as this will help to preserve as many elements of the original biota and ecological function as possible (Lunt and Spooner 2005). Therefore, despite a lack of *Eucalyptus* recruitment in conservation reserves on private land (Chapter 3), these areas are likely to be important for the preservation of valuable elements other than overstorey trees.

Conservation strategies, to date, have most commonly used plants from local provenances for the restoration of degraded fragments. This strategy has been widely accepted under the understanding that local populations are best adapted to local conditions (McKay *et al.* 2005) and to avoid deleterious genetic effects such as outbreeding depression in local provenances (Larcombe *et al.* 2016). However, in severely degraded or fragmented landscapes adequate high-quality seed may not be available (Broadhurst *et al.* 2008). As highlighted in Chapter 3, trees within reserves in a heavily modified agricultural matrix are overwhelmingly old and are likely to demonstrate reductions in reproductive fitness. Additionally, local provenance individuals do not provide insurance against extreme changes in climate that are predicted to occur by the time these seedlings mature. Using ecological niche modelling, restoration ecologists could select from species or genepools that will be suitable for the current climate *and* that of the future (Butterfield *et al.* 2017), therefore restoring ecological structure and function. Suitable restoration species may be present locally or be sourced from adjacent regions, eliminating the need for the introduction of exotic taxa. Provenance trials conducted in the Midlands have explored the performance of local and non-local genetic lines in restoration plantings (Bailey *et al.* 2013). Early results indicated that *E. pauciflora* seedlings from populations in hotter regions grow more rapidly and are less susceptible to frost and insect attack than local populations (Bailey *et al.* 2013). Twenty-five-year-old plantings of mixed provenance *E.*

gunnii-archeri have demonstrated that local plants survive poorly in the long term compared to individuals from a warmer provenance (Prober *et al.* 2016).

Future climate

In addition to recruitment failure, tree populations within the Midlands are threatened by climate change (Harris *et al.* 2015). In a high emissions climate change scenario (A2), temperatures across Tasmanian are projected to increase by 2.6 to 3.3°C evenly across the island. While no change in total precipitation is predicted for Tasmania as a whole, the spatial distribution and seasonality are expected to change. Annual rainfall is likely to increase over coastal areas but significant decreases are likely in central Tasmania including the Midlands (Harris *et al.* 2015). Seasonality of rainfall in the areas that support temperate grassy woodland and grasslands will change, with autumn rainfall projected to increase while spring rain is projected to decline. Hotter and drier conditions in the Midlands are predicted to cause declines in *Eucalyptus* cover due, in part, to the changes in water balance (Williamson *et al.* 2014).

In this study (Chapter 2) I predicted that up to 0.64 Mt of carbon could be lost by 2070 due to the loss of *Eucalyptus* species (Romanin *et al.* 2015). Changed climatic conditions will affect recruitment, increase mortality and reduce growth rates (Williamson *et al.* 2014). Altered conditions are likely to encourage a suite of additional impacts on soil properties, nutrient cycling and fire regimes (Harris *et al.* 2015). The community of plants best adapted to future conditions may be completely different to the communities being protected today.

Temperate grassy woodlands are vulnerable, in part, due to the inability of eucalypts to track a rapidly changing climate (Booth *et al.* 2015). Eucalypts are poor dispersers (Booth 2013) and are long lived so cannot rapidly evolve to match changing climate conditions. Hybridisation between species plays a minor role in speciation and dispersal of eucalypts (Potts and Reid 1988). Eucalypts are adaptable, but this will not be enough for populations to keep up with the speed of climate change. Assisted migration of eucalypts to suitable habitat may be essential to prevent species from becoming threatened with extinction in a hotter and drier climate (Booth *et al.* 2015). To retain trees in the Midlands it may be necessary to introduce

species that have never grown in the region but possess greater tolerances to hotter and drier future climate conditions.

Conservation programs are not designed for the uncertainty that is inherent in predicting future climate and altered species distributions in response to changed climate conditions (Harris *et al.* 2015). The future of nature in the Midlands will be reliant on the adaptive capacity of conservation programs and landowners. The region will require conservation and restoration that recognises rapid spatial changes (Hobbs *et al.* 2014). Within the Midlands, taking into consideration the uncertainty caused by climate change, it makes little sense to focus on conservation of small remnant patches, whether on private or public land. The most pragmatic approach is to consider the whole landscape. Importance needs to be placed on connectivity between individual remnant patches and as well as preserving natural values outside of these reserved areas (Gilfedder 1990; Mokany *et al.* 2006; Lechner *et al.* 2015).

Novel ecosystems

In this agricultural landscape with exotic species, a lack of natural regeneration, and where non-local species may be outperforming the locals, novel ecosystems have begun to evolve. Novel ecosystems are relatively stable assemblages of species that have not historically co-occurred (Bridgewater *et al.* 2011). Novel or altered ecosystems will be essential in future adaptation to climate change, providing habitat for important species to migrate through the landscape to suitable climate conditions (Hobbs *et al.* 2014). Novel ecosystems may include restoration plantings of species suitable for the future climate, or carbon sequestration plantations like those modelled in Chapter 2 (Chapter 2.3). Novel ecosystems will assist in the conservation of ecosystem services (e.g. carbon sequestration, water production and purification, nutrient cycling, food, fibre) within highly disturbed landscapes (Clement *et al.* 2017) where preservation of specific communities is unfeasible.

Land use, climate change and species invasions are all contributors to the formation of novel or hybrid ecosystems (Hobbs *et al.* 2014). Novel ecosystems have the potential to provide buffers and corridors in order to protect and connect isolated patches of remnant vegetation against climate change effects and

other abiotic and biotic threats. They can be a means of preserving genetic resources as insurance in a time of rapid change (Bridgewater *et al.* 2011; Hobbs *et al.* 2014).

As an example, temperate grassy woodlands that have lost their tree cover but retain an intact ground layer are valued as areas of lowland grasslands or potential habitat that grassland elements may shift to in the future (Harris *et al.* 2015). Novel or altered ecosystems may play an important role in future adaptation to climate change, providing suitable habitat for species on the move as a consequence of changed climatic conditions (Porfirio *et al.* 2014; Williamson *et al.* 2014; Raymond *et al.* 2015). Determining whether conservation effort in the Midlands is focussed on compositional or functional aspects of biodiversity is a social and political question as much as an ecological one (Hobbs *et al.* 2014). Using ecological niche modelling, restoration ecologists can identify species likely to be suited to future climate as a guide to restoring structure and function (Butterfield *et al.* 2017).

I estimated, using climate changed models and allometric equations, what the Midlands of the future could look like if a change in priorities led to massive replanting for carbon storage (Chapter 2.3). In this 645 km^2 study area I predicted that 2 – 2.7 Mt carbon could be replaced in the landscape by planting wide strips of vegetation covering 28% of the region (Romanin *et al.* 2015). This area would need to be taken out of production and added to the areas of native vegetation that remain in the landscape, and in that paper I suggested that surrendering such a large area of agricultural land to carbon storage would be unlikely in the Midlands landscape (Romanin *et al.* 2015).

However, since that paper was published, similar scenarios have been developed for the Tasmanian Midlands landscape in consultation with local stakeholders whereby intensification of agriculture could allow an increase in the area of land protected for biodiversity conservation (Carter *et al.* 2017). Farmer profitability and social and human capital were identified by stakeholders as being the most uncertain, but also most influential, aspects of the landscape (Carter *et al.* 2017). The authors were surprised to find that the area devoted to conservation could be highest when farmers were profiting most from their agricultural enterprises. The effects of extra irrigation water could positively impact on floodplains and ephemeral wetlands and increase their value for water storage and conservation. This is an example of the

land sparing concept whereby intensification of agriculture in defined areas leaves land spare for conservation in the remainder (Introductory chapter; Green *et al.* 2005). Despite these scenarios being hypothetical they are plausible and signal the beginning of a conversation between policy makers, land managers and stakeholders about future visions for the Tasmanian Midlands.

Conclusions

The Midlands of Tasmania is a cultural landscape. Humans have inhabited and modified the landscape for some 40,000 years. When Aboriginal people arrived in the Pleistocene, the environment they encountered was cold and harsh. Aboriginal people used fire as their primary tool for manipulating the landscape. By the time Europeans arrived in Tasmania in 1803, Aborigines had developed a harmonious relationship with the land.

Despite expectations that Aboriginal 'fire stick farming' was important (Jones 1969; Gammage 2008), this study found scant evidence of the use of fire throughout the Midlands in the 400 years prior to European settlement. This casts doubt on the relative importance of Aboriginal use of fire in the management of this landscape in the recent past (Chapter 1). This means that the question of how Aboriginal people managed the Midlands landscape remains unresolved and potentially unresolvable without new methodologies.

When European people arrived in Tasmania in the early 1800s they sought to change the land to suit their needs. I found clear and compelling evidence that Europeans used fire enthusiastically to manipulate the landscape in the first decades after settling the island. The magnitude of European burning in the sediment record far exceeded that of the recent Aboriginal period. This pattern of European land management being incongruent with that of indigenous peoples is repeated globally. It has been seen in tropical savannas as well as in the seasonally dry forests of mid-latitude USA (Bowman *et al.* 2011) and New Zealand (Perry *et al.* 2014).

Globally there has been an acceleration of human impacts since mid-20th C. Rapid increases in land clearance, greenhouse gas emissions, human populations and the surface temperature of the earth are well documented (Steffen *et al.* 2015). I was able to detect the trajectory of land clearance in the Midlands, from easily cleared, open and fertile temperate grassy woodlands first, to denser vegetation on infertile

soils much later. I found evidence (Chapter 2) that the first Europeans preferentially cleared the open temperate grassy woodlands to make room for increased agricultural productivity. Despite this significant change however, the total amount of carbon removed from the landscape was low because of the low density of trees. Denser temperate grassy woodlands and forests were cleared much later, around the 1940s, when more efficient mechanisation and fertilisers were available. The amount of carbon removed from the landscape increased rapidly after this time because denser vegetation was targeted and more extensively cleared. Rapid changes during the Anthropocene have been dubbed the 'great acceleration', and I present here evidence that this small island in the Southern Hemisphere is also greatly impacted by its effects with three times the carbon released in the 75 years between 1940 and this study than was released in the previous 140 years.

Various programs have evolved to preserve areas of native vegetation within this landscape and many land owners have established small reserves on their properties. In a landscape mostly in private hands, it is encouraging to witness a shift towards valuing the native vegetation of the Midlands Despite this, I found that many of these private conservation reserves are ineffective in protecting overstorey components of temperate grassy woodland (Chapter 3).

Simply fencing a remnant from stock grazing does not promote spontaneous improvements in vegetation health. The legacy of 200 years of European agriculture has altered recruitment dynamics so much that severe recruitment bottlenecks are apparent. Increased temperature and altered precipitation, predicted as effects of climate change, will further challenge the persistence of remnant vegetation.

Landowners and natural resource managers will need to determine whether their conservation efforts in the Midlands prioritise the historical state, i.e. species composition, endemism and biodiversity or whether they will work towards a novel future, i.e. functional composition and ecosystem services. For the Midlands to retain elements of native vegetation in the future, land owners and policy makers may need to consider radical changes and borrow from traditional agroecological systems of Europe such as the Dehesa and others discussed in the introduction to this thesis.

Using heterogeneous management techniques, such as grazing and patch burning, may provide niches for native elements (flora and fauna) to persist while preserving ecological functions (Leonard *et al*. 2010). Restoring the ecosystem functions of woodlands and grasslands may be more easily achieved and more valued than the conservation of individual species, while placing primary importance the composition of treeless grasslands would exclude the important ecosystem services that temperate grassy woodland communities provide in the face of future climates (Eldridge and Freudenberger 2005; Fischer *et al.* 2010). Assisting these landscapes to shift to a new biodiverse and stable state would take considerable effort and time, but this presents an opportunity for stakeholders to shape a Midlands landscape that would be resilient into the future, a landscape that includes well connected patches of native vegetation throughout an agriculturally productive and sustainable landscape. This constantly changing landscape is on the brink of a crucial new phase. Policies and practices chosen today will determine whether a new resilient stable state is achieved in the future.

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